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Title:
A study of the social behaviour and ecology on the wild Barbary macaque, Macaca sylvanus
A STUDY OF THE SOCIAL
BEHAVIOUR AND ECOLOGY
OF THE WILD BARBARY
MACAQUE, MACACA SYLVANUS L.

JOHN MAXWELL DEAG

DISSESTATION PRESENTED IN PART FULFILMENT
OF THE REQUIREMENTS OF THE DEGREE OF
DOCTOR OF PHILOSOPHY IN THE UNIVERSITY
OF BRISTOL, MAY 1974.

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I declare that the design and execution of the studies on which this dissertation is based are my sole and unaided work unless otherwise indicated and acknowledged in the text, and that no part has been submitted for any other degree at any university.

[Signature]
After coming together in the presence of a baby, four males remain in close proximity. A subadult male grooms an adult male (lt.) and a juvenile male grooms a second subadult male who cradles the baby male (rt.).

(From lt. to rt. AM1, SM2, SM1, BM2 at 10 weeks, JM1, group 6).
This appendix was added after discussion with my examiners Professor R.A. Hinde and Dr. N. H. Freeman.

1. In this thesis my aim (p7) was to arrive at a detailed analysis of the whole spectrum of behaviour within a monkey group and to examine its ecological background. This (and the lack of previous work on this species) necessitated the detailed qualitative and quantitative analysis that contribute to the excessive length of the thesis. Perhaps the most important parts are the social behaviour chapters (chapters 10, 11, 12 and 14). Chapter 15 is a synthesis of the results. The reader is advised to start with the abstract (pxxii) and to treat chapter 8 as an appendix. Three deletions (or changes) have been made to the original text (p 45, 76, 269).


Caution is advised in the interpretation of the results from this data.

(i) The aim was to provide a description of the group averaged over most activities. Some activities were excluded (p 378). For all animals, records were spread across the day (p 379) and hence different activities were included. Since, however, the relative frequency of animals participating in different activities was not more strictly controlled the results bear an unknown relationship to the actual distribution. An alternative method would be to collect separate records of animals engaged in particular activities (e.g. feeding, non-agonistic social interaction) or to sample activities in proportion to their relative frequency.

(ii) There is an unknown level of interdependence between the results in tables 13.1 and 13.2. For example, a score in one column may be partially determined by a score in another. The significance levels quoted for goodness of fit tests on this data (tables 13.3, 13.4, 13.5 (mothers), 13.6 (mothers) and p 392) are therefore not strictly accurate.

3. Other statistical tests.

In several places goodness of fit tests were done in cases where the data in the different categories were not strictly independent. The extent of the interdependence varies, but in each case it reduces the confidence that can be placed on the significance levels quoted. These tests have been eliminated (tables 5.3, 5.5, 10.8, 10.10, 10.14, 10.15, 10.17, 10.18, 10.21 and p 311). Their absence has little effect on the conclusions drawn.
Lack of independence between matrix cells means that tests on the distribution of social gestures between individuals (p 427 must be interpreted with caution.
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A STUDY OF THE SOCIAL BEHAVIOUR AND ECOLOGY OF THE WILD BARBARY MACAQUE, MACACA SYLVANUS L.

ABSTRACT

of a dissertation presented by JOHN MAXWELL DEAG in part fulfilment of the requirements of the degree of Doctor of Philosophy in the University of Bristol, May 1974.

This dissertation describes a field study of the social behaviour and ecology of the wild Barbary macaque Macaca sylvanus. It was carried out during 1968 and 1969 in a cedar forest in the Moroccan Middle Atlas Mountains. [See Appendix B]

CHAPTER 1: INTRODUCTION. The various types of field studies of macaques are discussed and it is suggested that more attention should be paid to the relative participation of individuals in several types of social interaction, absolute frequencies of social interaction, the relative sociability and proximity of individuals, communication, the function of social interactions, and obtaining larger samples of ecological data. The present study was orientated towards some of these points.

In the present and past centuries there has been periodic interest in Macaca sylvanus but behavioural work did not commence until 1964. This project represents the first detailed research on the species in the wild. I aimed to locate a wild, undisturbed population, make a preliminary study of its ecology and behaviour and then a detailed quantitative analysis of the behaviour of one group. For the latter, two methods were used, one based on social interactions and the other on the relative distance between individuals. Data was collected in such a way that the results from each method could be directly compared.

CHAPTER 2: DISTRIBUTION AND HABITAT. The Barbary macaque lives in isolated populations scattered in mountainous areas of Morocco, Algeria and Gibraltar. Its distribution and habitat in these areas are discussed. In Morocco it is found in cedar forests and holm oak forests in the Middle Atlas, more open mixed forests in the Rif, and oak and juniper scrub on steep slopes and gorges in the High Atlas.
The study area at Ain Kahla (Morocco Middle Atlas Mountains) was in a cedar forest in a dolomite - calcite region. Other trees include holm oaks and junipers and there is an important herb layer but no shrub layer. More open areas on the edge of the forest have numerous herbaceous plants not found under the trees and it is suggested that monkeys feeding outside the forest were exploiting these species. There is a Mediterranean climate modified by altitude. Most of the rain (mean = 855 mm p.a.) falls from October through March. Winters are severe with up to 4½ hours less daylight than summers, snow and minimum temperatures below freezing for up to five months of the year and down to at least -18°C. June to September it is hot (31°C) and dry. The forest is exploited commercially and semi-nomadic herdsmen graze cattle and sheep there during the summer.

The factors determining the distribution of the species are discussed. It is suggested that macaques can survive temperate conditions by having catholic feeding habits and a correspondingly generalized body structure. Man is probably primarily responsible for the present discontinuous distribution of the species.

CHAPTER 3: POPULATION STRUCTURE. The criteria used to distinguish age-sex classes are given and compared with those used for other macaques. At Ain Kahla the monkeys lived in multimale groups of 12 to 36 individuals (mean = 24). Larger parties were seen but experience showed that they contained two groups. The overall ratio of adult and subadult males: adult females was close to unity. Details are given of the 25 animals in group 6 - the group subsequently discussed in detail.

Population density was estimated to be 60 - 70 monkeys per km². The groups had home ranges that overlapped extensively; apparently no group had exclusive use of an area. Group 6's home range was 1.17 km². People were the only predators known to be successful.

Between late January and August the animals moulted. Copulation occurred during the autumn and winter; births in the spring and summer. There was a seasonal reduction in female receptivity that was independent of lactation. Females did not give birth every year; a 1:0:9 ratio of females suckling young was due to infants and babies from different years both nursing. Factors determining the interbirth interval are discussed.
CHAPTER 4: DAILY ROUTINE AND USE OF HABITAT. Group movements and daily routine are described. During the summer the day-journeys (principally accomplished on the ground) had a mean length of 1.53 km with a mean distance of 0.54 km between sleeping sites. In the summer the general pattern of movement was a peak of travel-feeding in the morning and afternoon with reduced movement and more time spent in the trees around midday. In winter this midday 'rest' period was reduced or absent. The initiation of group movements by adult males is described. Groups used numerous sleeping sites. Group 6 spent 90% of its daylight time in only 50% of its home range and stayed longer in those parts of its home range it entered frequently. The first 32% of the home range which accounted for 75% of the entries to hectare quadrats was termed the core area. This contained 80% of the sleeping sites and its perimeter was associated with the group's performance during intergroup encounters. It was not associated with any major differences in the distribution of resources. 13% of the home range was used each day. The relationship between the area used on successive days suggested an avoidance of areas recently used and this was investigated quantitatively.

CHAPTER 5: INTERGROUP ENCOUNTERS. Intergroup encounters were varied in type but could be arranged on a scale of increasing tendency for the groups to remain in each other's proximity. The outcome of an encounter depended upon the identity of the groups and possibly upon the context of the encounter. The mean duration of encounters was 86 minutes. Group 6 had approximately 0.05 encounters/hour. Many encounters occurred on the edge of the group's core area. Approximately 50% of encounters included overt agonistic behaviour between animals from different groups. Adult and subadult males played a major part in encounters. They participated more frequently than other age-sex classes in the intergroup behaviour which included tree-shaking, agonistic behaviour and intergroup monitoring. The latter involved a decisive move by an individual towards another group, followed by a prolonged period of sitting and watching in the zone between the groups. In other macaques, adult and subadult males also play a major part in encounters. Several of the encounter
types have been observed in other macaque populations. In provisioned populations the relative frequency of approach-retreat encounters may be exaggerated by the localized resources. The results are discussed in terms of the wide variety of factors likely to influence the nature and frequency of encounters in this and other macaques.

CHAPTER 6: FOOD AND WATER. The monkeys were entirely dependent upon natural food and water. Most feeding occurred on the ground. 70 food plants were identified. Many items were seasonal and their diet varied considerably throughout the year. Cedar trees provided several different types of food; leaves, seeds, seedlings, cambium, phloem, and male flowers. Many food items required considerable manipulation and the techniques used to exploit the plants were related to the anatomy of each species. Stones were repeatedly turned and animals and (particularly in winter) young, fresh, etiolated shoots found and eaten. Animals eaten included scorpions, grasshoppers and caterpillars.

Some home ranges did not include a permanent water supply. The monkeys drank from temporary sources in rocks and trees but it seemed that in some summers these dry up and all groups are forced to move to permanent sources. Water was usually drunk directly but they also ate snow, licked vegetation and dipped their hands into water in inaccessible places.

The monkeys damaged the cedars by removing the bark. Compared, however, with other demands on the forest (and the damage caused by grazing) the resulting loss of timber must be extremely small.

CHAPTER 7: RESPONSES TO PEOPLE, PREDATORS AND OTHER ANIMALS. A variety of responses to people and predators (jackals, dogs, foxes and possibly birds of prey) are described. The sighting of a person or mammalian predator was followed by barking and flight to the nearest trees. They were constantly alert while feeding and 'false alarms' were frequently produced by other stimuli. Vigilance behaviour (moving into a prominent position and sitting and watching the potential predator) was chiefly performed by adult males. Infants and babies were rescued by their mothers and adult males when they were isolated from the rest of the group. Special caution was
adopted while crossing open ground. Behavioural changes associated with habituation to the observer are described.

It is suggested that life in a multimale group in this forest species may be an advantage to reproductive males; several males may be available for the potentially dangerous activity of vigilance behaviour and thereby (indirectly) protect each other's young.

CHAPTER 8: BEHAVIOUR REPertoire. The criteria used to define the behaviour patterns are discussed. Patterns thought to be communicative are defined primarily by their structure and not function; for each pattern details are given of context and the responses of other animals. The species has a rich and varied repertoire showing many similarities with other macaques. The relationship is examined between the function of calls given by babies and infants and the function of similar calls given in different contexts by older animals. Non-communicative behaviour patterns are also described.

Most of the unique or especially developed patterns in this species were components of the unique male-baby-male social interactions described in chapter 12. The species also has a unique expression used in threat.

CHAPTER 9: INTRODUCING THE STUDY OF SOCIAL INTERACTION. The methods used to sample the distribution of social behaviour between the 25 individuals in group 6 are discussed. The technique involved recording all of the social behaviour visible to the observer during timed observation sessions (continuous recording sessions). This method was selected in preference to following the behaviour of one individual at a time because it focused on social interactions and the flow of behaviour between individuals, rather than intra-individual behaviour. A social interaction was defined as a continuous bout of continuous social behaviour between two or more individuals. 3192 interactions were collected at a mean rate of one every 2.7 minutes. The analysis presented in subsequent chapters is based on 1740 of these (spread throughout the daylight hours) from the non-mating season. It is recognized that there are several potential sources of bias in the data collection and these are discussed. The data was examined using a computer programmed to permit analysis in terms of the
frequency of events (or combinations of events), the frequency of behaviour patterns being used between individuals and transitions of behaviour between and within individuals.

CHAPTER 10: AGONISTIC BEHAVIOUR. An analysis is presented of the context and distribution of agonistic behaviour between individuals in one group during the non-mating season. All the behaviour occurred naturally; none was induced by feeding. Animals passively avoided monkeys which threatened them on other occasions and the distribution of dyadic passive avoidance and dyadic threat was used to define basic rank and the social hierarchy. This was basically linear with one major reversal. Apart from a few more reversals the distribution of threats, chases and attacks in situations involving more than two animals was similar to dyadic threats. The possible functions (submission, appeasement, greeting, reassurance, calming, enlistment and assertion of rank) of non-aggressive behaviour in agonistic interactions are defined and examples given.

The frequency of giving aggression and receiving passive avoidance were positively correlated with basic rank; aggression received and passive avoidance given, negatively correlated. The ratio of aggression given: received and passive avoidance given: received varied in different parts of the hierarchy. For the top eight animals these ratios were better predictors of status than the frequencies of behaviour. Adult males were unique; they received little aggression and gave little passive avoidance but respectively gave and received a lot of these.

The frequency of behaviour typically given or received by the dominant of a pair was generally more highly correlated with basic rank. Behaviour typically given by the subordinate was generally the most constant in direction showing particularly few reversals. My results confirm Rowell's opinion that subordinate animals play a major role in maintaining the social hierarchy. They also show that the importance of aggressive behaviour in producing a hierarchy should not be underestimated; aggressive and submissive behaviour differ in their relative importance in maintaining relative status in different parts of the hierarchy.
CHAPTER 11: THE BEHAVIOUR OF MOTHERS, OTHER FEMALES, BABIES AND INFANTS. The interbirth interval resulted in two categories of unweaned monkeys (babies and infants) being present for much of the year. From the first week of their life babies (and later infants) were regularly involved in social interactions with other females (chiefly juveniles and subadults). Females approached mothers with babies and infants and also cared for babies in their mothers' absence. Juvenile and subadult females carrying babies approached and were approached by other young females. Females interacted frequently, but not exclusively, with particular mothers and their offspring. Infants, in the absence of their mothers, were treated more like juveniles. Play was restricted to subadult and younger animals with the youngest playing most. Play situations, play initiation, play termination and play components are described.

Over the first few months the two mothers studied in detail spent between 50 and 90% of their time with their babies interacting with other monkeys. About 95% of the friendly approaches received by mothers of babies were in the presence of their babies; for mothers of infants the corresponding figure was 70-80%. In contrast to other age-sex classes mothers, babies and adult males received more friendly approaches than they gave. Allogrooming was unevenly distributed between females. Mothers, babies and infants received most grooming and generally received more than they gave.

The function of non-maternal female interaction with babies, infants and their mothers is discussed and compared with that of other macaques.

CHAPTER 12: SOCIAL INTERACTIONS INVOLVING MALES, BABIES AND INFANTS. In the study population there was more male interaction with babies and infants than has been described for other cercopithecoida. Adults, subadult and juvenile males participated with them in several types of interaction. This occurred during the babies' first week of life and continued until they were about 1 year old. Males interacted with mothers with young babies; cared for babies; carried them to other males, or were approached by them and close interaction followed ("type b interactions"). Juvenile males played with babies and infants and some play components were clearly related to type b interactions. Males did not interact equally with all babies but the basis for individual preferences is unknown.
A major part of the chapter is devoted to describing the most interesting and unique type b interactions and testing the 'agonistic buffering' hypothesis on their function. This hypothesis proposes that the use of babies and infants in encounters between males allowed relatively subordinate animals to regulate and/or stabilize their relations with those more dominant to themselves. The influence of a baby's presence on the behaviour of males is examined quantitatively and is shown to determine many aspects of male-male interaction. For example (1) 77-100% of the friendly approaches given and 71-97% of those received by males to and from other males were in the presence of babies. (2) 81% of the grooming between males occurred in this context. (3) Between unlike age-classes and between adult males, a male carrying a baby to another was usually subordinate. (4) Most approachers to males with babies were also subordinate. (5) Some approachers were threatened but it seemed that they risked this to have the possibility of interacting with males who could otherwise rarely be approached.

It is suggested that compared with some other macaques the less violent agonistic behaviour of this species, the lack of solitary males and the absence of the exclusion of young males to the periphery of the group, may be related to this behaviour. Male-male agonistic buffering in other species and its evolution are discussed.

CHAPTER 13: THE SPATIAL DISTRIBUTION OF GROUP MEMBERS. Group 6 is described in terms of the relative proximity of group members to each other. The three main ways that have been used to describe or imply the relative proximity of individuals in groups are discussed. A nearest neighbour method was used to equally sample all individuals in group 6.

Many of the possible subject - neighbour pairs occurred but it was noticeable how frequent certain pairings were. Using first neighbours only and first three neighbours together, sociograms were drawn to show which animal's contributed a major proportion of each animal's total neighbours and subjects. Tests were conducted to see if a subject's first neighbours were drawn at random. The associations between individuals are summarized. Individuals showed their own specific associations each having different associates.
from the other members of its age-sex class. The members of a class frequently showed a close similarity in the age-sex class of their associates. Younger animals (except babies) and adult females with no unweaned offspring, occurred as neighbours less often than expected and were therefore, by inference, relatively further on average from their neighbours. There was a positive correlation between frequency as a neighbour (and hence proximity) and basic rank. All juvenile and subadult males had significantly more male neighbours than expected; such a clear sex preference set them apart from the other animals. The influence of one neighbour (unweaned monkeys) upon others (males and mothers) was investigated.

There was no indication that particular individuals were regularly restricted to the group's spatial centre or periphery. The central - peripheral arrangement of group members in other macaques is discussed and factors promoting peripheralization examined.

CHAPTER 14: GENERAL CHARACTERISTICS OF SOCIAL BEHAVIOUR. The diurnal distribution of social behaviour in the summer is examined and compared with other aspects of the animal's routine; peaks of agonistic behaviour, for example, corresponded with peaks of foraging. 47% of all social interactions included agonistic behaviour, 20% maternal behaviour, 10% play, 39% other non-agonistic behaviour involving infants or babies. Most interactions involved only two individuals; threes and fours also occurred but interactions larger than this were rare. Animals differed in the frequency with which they participated in social interactions; participation of adult females was related to whether they had babies, infants, or no unweaned young.

Individual associations based on mutual participation in social interactions and the exchange of social gestures are investigated. Apart from a few exceptions they revealed similar associations to the nearest neighbour data.

Individuals did not send or receive signals at random or in proportion to their relative sociability. Certain age-sex class preferences were prominent. The associations between classes are compared with those described by Altmann for *Macaca mulatta*. 
There was a positive correlation between proximity (as defined by the nearest neighbour study) and the probability of interacting, giving and receiving social gestures.

CHAPTER 15: SYNTHESIS: THE SOCIAL ORGANIZATION OF MACACA SYLVANUS AT AIN KAHLA. After discussing the multifactoral nature of social organization, intragroup behaviour is summarized and its function examined. Age-sex classes in group 6 had different (but overlapping) activity profiles and distributed their behaviour differentially between the other classes. Classes differed in the extent of intra-class variability; several causes of variability are suggested. The definition of 'social roles' is discussed. The role categories often recognized for macaques are summarized and their applicability to group 6 examined. For this group it was only useful to recognize different adult female roles (the mother role; the childless adult female role). The behaviour of other so called role categories was in fact typical of whole age-sex classes.

The function of social behaviour is examined bearing in mind the genetic theory of natural selection. The social behaviour of these monkeys can be explained with hypotheses based on behaviour increasing individual fitness (promoting the survival of the individual and its offspring), kin-selection and misplaced reproductive behaviour. The latter may be particularly prevalent in macaque societies because of the "paternity problem", males do not know their own offspring. Group functions and the functional organization of groups are investigated.

Comment is made on methodological problems hindering major advances in primate field studies.

APPENDIX A: SEXUAL BEHAVIOUR. Preliminary conclusions are presented on the participation of group 6 monkeys in sexual behaviour.
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1. INTRODUCTION

This thesis describes a field study of the social behaviour and ecology of the wild Barbary macaque *Macaca sylvanus*. It was carried out during 1968 and 1969 in a cedar forest in the Moroccan Middle Atlas Mountains.

1.1. TAXONOMY OF *MACACA SYLVANUS*.

Genus *Macaca* Lacépède 1799.
Species *Macaca sylvanus* Linnaeus 1758.

Common names. Barbary macaque, Barbary ape, Gibraltar macaque, Gibraltar ape, Le magot. For local names in N.W. Africa see Cabrera (1932) and Joleaud (1931b).

For synonyms of *Macaca* and *Macaca sylvanus* see Allen (1939), Didier and Rode (1936), Cabrera (1932), Ellerman and Morrison-Scott (1951), Elliot (1913), Forbes (1897), Napier and Napier (1967), Rode (1937) and Trouessart (1900).

Most recent authors (e.g. Burton, 1972; Deag and Crook, 1971; Hill, 1966; Lahiri and Southwick, 1966; MacRoberts, 1970; Napier and Napier, 1967) have used the specific name *Macaca sylvana*. Others (e.g. Hill 1970)* have used *Macaca sylvanus*. According to J.R. Napier (personal communication) *sylvanus* is the correct form, since specific names which are proper names - Sylvanus was a god - do not have to agree with the sex of the generic name. *Macaca sylvanus* is the type species for the genus.

No subspecies or geographical races have been named. It is sometimes stated that specimens from Morocco are redder than those from Algeria. This arose from the observations of P. Bede (quoted by Joleaud, 1931a; Cabrera, 1932). Rode (1937) found there was no difference between Algerian and Moroccan skins.

* and Thorington and Groves, 1970.
1.2 ASSESSMENT OF MACAQUE STUDIES

1.2.1 Field studies of macaques

The following is not intended to be a comprehensive review of field studies of macaques. The purpose is to illustrate the nature of these studies in order to indicate why I adopted my own particular approach during the present project. Most of these comments could be applied to field studies of other primates. Macaques are probably the most studied of non-human primates, both in and out of the laboratory. Field studies have not, however, been equally distributed between species. Most effort has been concentrated upon the rhesus (M. mulatta), chiefly by American workers in India and on the feral populations on Carribean islands (Cayo Santiago and La Parguera) and on the Japanese macaque (M. fuscata) by members of the Japan Monkey Centre. It is regrettable that so little has been published in English on unprovisioned Japanese monkeys.

General studies. These studies have described, at a preliminary level, the behaviour and ecology of a population or group. For social behaviour they usually include descriptions of behaviour patterns, the distribution of social behaviour between age-sex classes together with details of the behaviour of some individuals. Some quantification is often included (but with little or no attempt to develop unbiased sampling techniques) to show the relative frequency of different types of behaviour and the frequency with which individuals participate in different types of social interaction. Examples include, studies of rhesus (Neville, 1966, Southwick et al 1965); the bonnet macaque (M. radiata; Simonds, 1965; Rahaman and Parthasarathy 1969a, b; Nolte, 1955; Sugiyama, 1971), the Japanese macaque, (Imanishi, 1963; Yamada, 1966), the crab-eating macaque (M. fascicularis; Furuya, 1965a), the lion-tailed macaque (M. silenus; Sugiyama, 1968) and the pigtail macaque (M. nemestrina, Bernstein, 1967).
Population surveys. The only long term survey of a wild macaque population has been of rhesus by Southwick and his colleagues (Southwick and Siddiqui, 1968). These studies are valuable for the detection and understanding of demographic changes. There is also information available for the provisioned populations of Cayo Santiago (Altmann, 1962; Koford, 1966) and Takasakiyama, Japan (Carpenter and Nishimura, 1969).

Ecological studies. Hardly any studies have been aimed solely at ecological problems and this has led to rather scanty ecological data with conclusions based on small samples. For instance, very few studies record accurately the home-range size, or group counts with identifications, for more than a few groups. Hladik and Hladik (1972) included the toque macaque (M. sinica) in their study of food consumption.

Studies of specific aspects of behaviour. These studies have become more frequent now that there is background information on several macaques. It has also become difficult for a field worker to study more than one topic to the required depth. A few of the numerous examples include: In the Japanese macaque, grooming (Furuya, 1965b), vocalizations (Itani, 1963; Green, personal communication), the acquisition of new food habits (Kawamura, 1959; Tsumori, 1967), group division (Sugiyama, 1960; Furuya, 1968), sexual behaviour (Tokuda, 1961-62), novelty (Menzel, 1969), paternal care (Itani, 1959) and interbirth interval (Tanaka et al, 1970). In the rhesus, intergroup encounters (Vessey, 1968), adult males (Kaufman, 1967), extra-troop relations (Wilson, personal communication), sexual behaviour (Carpenter, 1942a; Lindburg 1967; Loy, 1970b, 1971), social communication (Altmann, 1962, 1965) and infants and mothers (Kaufman, 1966). In the Barbary macaque, sexual behaviour (MacRoberts and MacRoberts, 1966) and social development (Burton, 1972) and in the crab-eating macaque, social communication (Shirek-Ellefson, 1967).

Studies on the genealogical aspects of behaviour. There has been a growing realization that many affinities between individuals in groups and consequently much social interaction, is explicable in terms of matriarchal kinship and sib-relations. This approach, developed in
Japan (Yamada, 1963) has subsequently been followed by Sade and his colleagues. Examples include: In the Japanese macaque, social hierarchies (Kawai, 1958; Kawamura, 1958) and group division (Koyama, 1970). In the rhesus, social hierarchies (Koford, 1963a, Sade, 1967), grooming and subgroups (Sade, 1965), subgroups (Quiatt, 1966) and sexual behaviour (Sade, 1968) and in the Barbary macaque, protector-protege relationships (MacRoberts, 1970).

Studies on the relative sociability of individuals and age-sex classes. Most studies make some mention of this but only Altmann (1968) has attempted systematic quantification. His method used the relative frequency with which age-sex classes gave and received social signals. Data collection was spread over a period of two years and several groups. While the results described the relative sociability of age-sex classes in the population, they were not intended to describe the relative sociability of individuals within one group. The lack of attention to this topic by field workers is surprising in view of Carpenter's early discussion of the problems and his development of formulae to permit description and comparisons (Carpenter, 1942b, 1952).

I believe that in addition to the types of study outlined above, field projects should pay more attention to the following points. These will not only aid our understanding of primate societies but will facilitate comparisons between populations and species. The present study was orientated towards some of these problems (sections 1.2 and 1.3.1).

(1) Promising ideas on the concept of social roles and their use as descriptive tools (Bernstein and Sharp, 1966; Kummer, 1967a; Gartlan, 1968; Reynolds, 1970; Crook, 1970) have not been preceded or followed by the development of adequate field techniques to sample social interaction in macaques. Several of the studies of specific topics mentioned above have achieved such measurement for a very narrow spectrum of behaviour. Some studies should therefore aim to develop satisfactory sampling techniques to show the relative participation of individuals in several types of social interaction or the relative frequency with which individuals give and receive particular social signals.
(2) The recording of absolute frequencies of specific types of social interaction and social signals. This is difficult owing to problems of visibility but is important for some comparisons.

(3) The development of techniques to describe aspects of a group's social organization based on the whole spectrum of behaviour (e.g. the relative sociability of individuals in a group or the relative proximity of individuals to each other). Such techniques will be important tools for comparative work.

(4) The nature of communicatory processes. There is now considerable knowledge of behaviour patterns that are probably communicative but there has been little attempt in the field, except for the work of Altmann (1962, 1965) (see also Chalmers, 1968, on mangabeys), to investigate quantitatively the relationship between signals, response and subsequent action by the signaler. Studies of this sort are bound to be complex and are incompatible with most other types of study. Care should be taken to control more exactly the data collection situation in order to separate inter and intra-individual transitions. This is difficult in a social setting (Slater, 1972, in press).

(5) The function of social interactions aided by the development and testing of suitable hypotheses.

(6) In one area of field primatology - the study of the relationship between ecology and social organization - there has been considerable theoretical advancement (Crook and Gartlan, 1966; Crook, 1970; Denham, 1971; Kummer, 1971; Eisenberg et al, 1972) and this has stimulated several field studies. There has, however, been an inadequate development in primate ecology to test the numerous hypotheses suggested. It is essential to commence long term studies of wild populations. In order to correct the current imbalance and obtain sufficiently large samples, some studies (of at least a year) should concentrate entirely upon ecological problems. These long term studies would be best carried out in reserves or national parks.
1.2.2 Studies of *Macaca sylvanus*.

In spite of this monkey being the closest to Europe, occurring on Gibraltar and posing a series of fascinating zoogeographical problems (section 2.3) it is only since 1964 that modern primatologists have taken an interest in it. The present project was the first detailed research on the species in the wild. Early accounts of the species have been summarized by Cabrera (1932), Hill (1966), Huard (1962), Morris and Morris (1967) and Reynolds (1968). During the great expansion in the study of natural history during the 18th and 19th centuries most accounts of the species (e.g. Darwin, 1872; Lydekker, 1894; Forbes, 1897; Sclater, 1900; Trouessart, 1900) were based on reports from Gibraltar, captive animals or from the observations of R.L. Desfontaines (Lydekker, 1894; Cabrera, 1932) who in the late 18th century observed the species near to the Algerian coast. These accounts include little information on social behaviour.

In the early 1920's Kearton (1924) visited Algeria, filmed and photographed the animals and provided one of the few modern accounts of their behaviour in the wild. He reported that in snowy weather they sought the more temperate climate of the gorges, described fight breaking, subgroups of nursing females, play (including intervention by mothers), the approach of squealing infants to adult males followed by huddling together, the prevention of suckling by mothers, the lack of wounds indicating the absence of severe fights and intergroup chasing. He also considered that each group had an 'old chief' who was the oldest animal and 'whose word or action is law'.

Around the 1930's there was considerable interest in the species as revealed by the work of Joleaud (1930-31, 1931a, b), Cabrera (1932), Didier and Rode (1936), Heim de Balsac (1936) and Rode (1937, 1947). Although most gave details of anatomy, diet, distribution and comparative zoogeography, only Cabrera gave a factual account of the biology of the species in the wild. Interest continued with the work of Frenchkop (1951), Zeuner (1952) and Panouse (1952). More recently the fossil history of this and related species has been clarified (references in section 2.3). Behavioural studies did not commence until 1964 when Lahiri and Southwick (1966) studied a colony
in the U.S.A. and MacRoberts (1970) studied the Gibraltan animals. Both studies recorded the frequent interaction between males and babies which had been mentioned previously by Lydekker (1894). MacRoberts and MacRoberts (1966) also studied the genealogical aspects of group organization and sexual behaviour. Following the present project Burton (1972) studied the social development of the Gibraltan animals for three months in 1970. Whiten and Ramsey (Whiten, 1972) studied them for a month during 1971 at Jbel Lakraa (fig. 2.3) in the Moroccan Rif in order to see whether agonistic buffering (Deag and Crook, 1971) occurred in that population.

1.3 AIMS.

My aims for this project were:

(1) To find a study site in Morocco away from human habitation, where the monkeys lived in a natural habitat, completely dependent upon natural food and exposed to a minimum of disturbance.

(2) To make a preliminary study of the population's ecology and behaviour in order to pinpoint features of interest and produce data which would put into perspective a subsequent, more detailed study of one group. For instance, unless a background norm for ecology and behaviour had been established for the whole population and an idea of intergroup variability obtained, it would not be known how far the data from one group could be generalized to the whole population or how details of one type of behaviour were related to the rest of the species' repertoire.

(3) To make a detailed quantitative analysis of the behaviour of one group. Earlier reports (above) had suggested that the interest of males in babies would be one profitable topic for specific study. Experience gained during the population study permitted me to define more exactly my aims for a study of one group. These are discussed in the following section.
1.4. METHODS.

1.4.1. Plan of the project.

I was in Morocco for 15½ months during which the project was structured as follows:

Survey. After arriving in Morocco on 22.6.68 my wife and I spent from 28.6.68 to 13.7.68 visiting sites in the Middle Atlas Mountains. During periods at the forestry posts of Tagounit, Ouiouane and Ain Kahla we searched much of the forest from Azrou, south to a line between Ouiouane and Timhadit. We soon found the Ain Kahla population that fulfilled my criteria for a wild, relatively undisturbed population and this made any further search unnecessary. The occasional search was made for monkeys in other parts of Morocco and extremes of habitat noted.

Preliminary study of the Ain Kahla population. From 22.7.68 to 16.8.68 we were joined by John H. Crook and a preliminary study was made of the Ain Kahla population (Deag and Crook, 1971). During this period we checked our methods of ageing and sexing the animals, uncovered several key problems and formulated our ideas on the importance of the frequent male - baby - male interactions. Following this we searched, with J.H. Crook, for the isolated population to the S.S.E. of Marrakesh (section 2.1.1).

Population study. From 6.9.68 to 13.5.69. During this and the subsequent period I made observations on my own at Ain Kahla and attempted to get to know as many groups as possible within the study area; to make observations on the ecology of the animals; to observe their behaviour in order to construct a repertoire of behaviour patterns and obtain protocols of social interactions; to test the quantitative methods that I would later apply to one group and to analyse the diurnal distribution of behaviour by means of individual activity records.
A study of a single group. Towards the end of the population study I decided to concentrate my observations on one group. I therefore started to quantify the behaviour of individuals in group 10, the group I was currently working with. This group was unexpectedly difficult to follow; prolonged periods of sitting and feeding were followed by swift movements during which I usually lost the group. It was difficult to relocate and it became clear that the desired level of quantification would not be achieved. Following a brief period during which I attempted to find a group that could be watched extensively, and experimented unsuccessfully with provisioning monkeys outside the study area, I relocated group 6. I had not worked with this group for three months but a crippled female made it easy to recognize and it proved easy to follow. I worked with the group from 13.5.69 to 7.10.69 (the end of the project) and although I continued with other observations when time permitted, I concentrated upon the following:

(1) During the population study it became clear that the distribution of behaviour between monkeys, the relative frequency of different types of behaviour, the function of the male - baby - male and other social interactions, the relative sociability of individuals, the diurnal distribution of social behaviour and so on, could only be adequately studied by adopting quantitative techniques that provided an unbiased sample of intra-group behaviour over a specified period of time and recorded participation of individuals rather than age - sex classes. The above features could then be examined and observed frequencies tested, where appropriate, against the values expected if individuals interacted at random. While it would be naive to expect randomness - in fact almost all definitions of society exclude it - this is at present the most realistic level at which to analyse macaque societies. In future one could test against non-random models constructed upon the basis of earlier studies.

(2) Primate groups are characterised by their high level of complex social interaction and the population study soon indicated that whatever method was selected to obtain an 'unbiased' sample of behaviour, the sample would possibly be coloured by the large volume of behaviour to be recorded, the method adopted or subject
to bias imposed by the observation conditions. While the first two might be minimised by adopting appropriate data collection techniques it would prove difficult to completely remove bias imposed by observational conditions (Aldrich-Blake, 1970). There was also a need to provide a simple technique (using data that could be gathered quickly and analysed easily) to describe the affinities between individuals in a group. Such a technique would greatly aid any future comparison between this and other populations or species and would also provide an independent check on the results from the analysis of social interactions. The population study showed that the spatial distribution of individuals relative to one another was non-random and a nearest neighbour technique was therefore developed to describe the spatial distribution of the group in terms of the relative proximity of individuals. Data for social interactions and the nearest neighbour analysis were collected separately with no one observation contributing to both sets of data. Except in as much as they were derived from the same group, the results were independent and a strict comparison is possible.

During the summer and early autumn we camped near to the forestry post; at other times of the year we used a room in the post. Over the winter, owing to the isolated position of Ain Kahla and the likelihood of being cut off by the snow we laid in supplies for three months. From the start of the population study onwards, I was absent from the study area (collecting supplies, servicing equipment, receiving medical attention, avoiding the army exercises in the area or holidaying) at the following times: 10.10.68 - 29.10.68, 8.3.69 - 17.3.69, 10.6.69 - 26.6.69, 24.7.69 - 9.8.69 and 9.9.69 - 25.9.69. Approximately 600 contact hours (time when I was with at least one monkey group) were obtained during the population study, 630 during the single group study of group 6 and during that period a further 10 hours with other groups. Excluding the survey and preliminary studies at least 1,240 contact hours were therefore obtained.

1.4.2 Observation techniques.

General observation techniques will be discussed here. Details of methods used to collect specific sorts of data are given in the relevant
sections. During the population and single group studies I worked in
the field alone and recorded data in field note books, on data cards,
maps or by tape recorder. Maps were copied out and all other data
transferred to duplicate note books. Tape recordings of vocalizations
were made. 16 mm. colour film was taken and has been made into a 30
minute film with sound, that traces the changing behaviour and ecology
of the population throughout the year (Deag, 1970). 35 mm. photographs
were taken. Binoculars were essential and a high powered telescope
occasionally useful.

I adopted the method of following a group moving deliberately,
slowly and in the open without hiding (chapter 7). With habituated
groups I could often get to within 20-30 m. or even as close as 3 m.
to the animals. I did not, however, work that close since it in-
creased the arc that had to be scanned to keep them under observ-
ation and at that distance there was always the danger of disturbing
the animals. I did not stare at individuals for long periods and if
they became disturbed I either looked away, ceased to follow, or gave
them time to settle down before continuing with data collection. The
numerous spurs and gullies helped observation since it was possible
to sit on one slope and watch the animals on the slope opposite. By
moving ahead of the group and sitting near to their predicted route
it was possible to get closer. With rare exceptions I attempted
to remain neutral and made no signals to the animals.

A group was usually located by the barks stimulated by my approach.
When they were out of sight contact could be kept by the sounds of
moving branches, the turning of stones and vocalizations. It was
possible to track them and determine the speed and direction of
movement from the characteristics of the holes they dug to extract
food items. Snow made tracking easy but during the winter observ-
ations were frequently curtailed by periods of heavy rain, snow, low
cloud or very cold weather. The movement of animals along the edge
of the forest and their visits to wells during some seasons also
facilitated location and observation. It was important, however,
to distribute the observations throughout the habitat and not to
restrict them to places where the animals were easy to find or see.
Their habit of adopting a new place to sleep almost every night meant
that to be sure of finding a group the next morning it had to be
followed to its sleeping trees the night before. In the early part of the project I used the Land Rover as a hide for watching unhabituated groups near to the tracks. Most of the filming was done without a hide; one was, however, used to get close-ups near to the sleeping trees.

1.5. SUMMARY.

The various types of field studies of macaques are discussed and it is suggested that more attention should be paid to the relative participation of individuals in several types of social interaction, absolute frequencies of social interaction, the relative sociability and proximity of individuals, communication, the function of social interactions, and obtaining larger samples of ecological data. The present study was orientated towards some of these points.

In the present and past centuries there has been periodic interest in *Macaca sylvanus* but behavioural work did not commence until 1964. This project represents the first detailed research on the species in the wild. I aimed to locate a wild, undisturbed population, make a preliminary study of its ecology and behaviour and then a detailed quantitative analysis of the behaviour of one group. For the latter, two methods were used, one based on social interactions and the other on the relative distance between individuals. Data was collected in such a way that the results from each method could be directly compared.
2. DISTRIBUTION AND HABITAT

2.1. GENERAL DISTRIBUTION AND HABITAT.

The Barbary macaque has a discontinuous distribution with isolated populations scattered in Morocco, Algeria and Gibraltar. Some authors (e.g. Zeuner, 1952; Napier and Napier, 1967) record it in Tunisia. This is incorrect but it probably lived there in historic times. (Joleaud, 1931a). Forbes (1897) wrote that the species lived on Gibraltar and some distance into Spain but I have not seen this confirmed by any contemporary article. Joleaud (1930-31, 1931a) and Cabrera (1932) described, and Heim de Balsac (1936) mapped, its distribution (fig. 2.1). During this project I made no attempt to completely survey the species' distribution in Morocco.

2.1.1. Morocco. *

Distribution. The species is found in the Rif, Middle Atlas and High Atlas. Of the earlier surveys Joleaud's (1931a) is the most comprehensive. Heim de Balsac omitted from his map (fig. 2.1) locations in the south and central Middle Atlas. Panouse (1957) mapped (using reports from officials of L'Administration des Eaux et Forêts) the species' distribution in Morocco. During the printing of his map the location of the Rif population was displaced to the west and I have therefore adjusted this in fig. 2.2. Whiten (1972) mapped the species' distribution in the western Rif (fig. 2.3). (Since these two maps do not correspond I may have overcorrected Panouse's map). Joleaud (1931a) and Cabrera (1932) give further details of the Rif population. Heim de Balsac's map shows the species extending towards Aknoul in the eastern Rif but I know of no recent reports from this area or the central Rif.

* A preliminary account has been published in Deag and Crook (1971).
FIG. 2.1.
Map of N. Africa showing the distribution of *Macaca sylvanus* (from Heim de Balsac, 1936).
FIGURE 2.2.
Map of Morocco showing the distribution of *M. sylvanus* (after Panouse, 1957) and the position of study sites. From Deag and Crook (1971).
Forestry Officials' reports of isolated populations of monkeys in Northern Morocco.

FIGURE 2.3.
Distribution of M. sylvanus in the Western Rif of Morocco. From Whiten (1972).
Most reports indicate that the macaques occur throughout the Middle Atlas. Here the most northerly location reported is S.W. of Taza and a little further south in the Jbel bou Iblane region (Joleaud 1931a). These areas were included in Panouse's map but I know of no more recent reports. I received reliable positive reports from further south, in the vicinity of Ifrane 14 km. N.E. of Azrou and N.E. of Boulemane, 45 km. east of Azrou.

Joleaud (1931a), Cabrera (1932) and Heim de Balsac (1936) recorded the species in the Ourika Valley (long. 7° 47'w, lat. 31° 18'n.), 50 km. S.S.E. of Marrakesh (fig. 2.2). Panouse (1957) had not included this area on his map. J.H. Crook and I visited the area and located a party of monkeys in the Ourika Valley to the south of the village of Setti Fatma at approximately 1,900 m. altitude. Several independent reports indicated that there were also monkeys above the village of Tourchte, likewise in the Ourika Valley. These localities appear to be the only places where monkeys live in this area. Joleaud (1931a) recorded that the species lived in the Goundafa (the region between Azni and Tizi-n-test south and S.S.W. of Marrakesh). J.H. Crook and I visited the forestry posts in that area but all reliable reports were negative. The Ourika population may represent the south-western limit of the species' range.

Habitat. A comparison between the above accounts of the species' distribution and descriptions of the climatic and vegetational features of the country shows that the vegetation is not uniform throughout its species' range. The Moroccan forests fall into various bioclimatic zones and the presence or absence of tree species may be taken as indicators of these zones (Metro, 1958). There is, in practice, no sharp division between the zones but rather a gradual change of species in association with latitude, altitude and climate. Examples of four contrasting habitats are now given. The considerable range of habitat suggests some interesting comparative studies.

(1) Cedar forests of the Middle Atlas. (Plate 2.1). An example of this habitat is discussed in section 2.2. The dominant tree species are cedar (Cedrus libanotica Link spp atlantica (Man). Holmb) mixed with various proportions of holm oak (Quercus ilex L.) and a juniper
15. *Ljuniperus thurifera* L.). Placed in the humid and subhumid zones (Metro, 1958) these forests receive considerable winter rain and snow. Examples include the forests to the south of Azrou (e.g. Ain Kahla and Ouiouane), near Ifrane and between Kenifra and Itzer. Cedars occur above 1,600 m. (Lepoutre, 1957-61).

(2) Oak forests of the Middle Atlas. (Plate 2.2). At a lower altitude than the cedar forests and in dryer areas, forests of almost pure stands of holm oak are found. Examples include the forests just above Azrou and Ain Leuh. These forests merge into the cedar forests and an example of this transition is found to the south of Tagounit. They receive considerable winter rain and some snow and are probably dryer than the cedar forests during the summer. In these localities the forests are on rounded hills and steep slopes without the ravines or high cliffs as seen in habitats (3) and (4). They may occur in some areas. There is no shrub layer and often little herbaceous vegetation. The forests are grazed and some adjoin cultivated land. Compared with the cedar forests the macaques were harder to see.

Further south to the S.E. of Beni-Mellal and at El Ksiba the forests are dryer and fall into the dryer parts of the sub-humid zone and the hot semi-arid zone. Typical tree species are the holm oak, *Pinus halepensia* Mill., a juniper *J. phoenicea* L. and *Tetraclinis articulata* (Vahl) Mast. I have not personally seen monkeys in these southern forests. Reliable positive reports were, however, received and the area is included on Panouse's distribution map.

(3) Mixed forests of the western Rif. (Plate 2.3). The description here is taken from Metro (1958) and Whiten (1972, personal communication). Tree species include the holm oak, the cork oak (*Quercus suber* L.), *Q. pyrenaica* Willd, *Q. faginea* Lam., *J. thurifera*, *Abies pinsapo* Boiss., *Pinus pinaster* Sol., and *Pinus nigra* Am., There were no cedars in Whiten's study area but they do occur in parts of the Rif. At Jbel Lakraa the forest is less dense than in habitats (1) and (2) and includes large open spaces and screes with sparse grassy vegetation and steep rocky cliffs up to 60 m. high. Snow falls occur in this area.
(4) Oak and Juniper scrub in the High Atlas. (Plate 2.4). The Ourika Valley lies in the hot semi-arid zone and the stunted vegetation is more accurately described as scrub than forest. The terrain consists of very steep mountain slopes and rocky gorges dissected by swiftly flowing streams. On the slopes grow stunted holm oaks, junipers (J. phoenicia) and ash bushes (Fraxinus) plus dwarf palms (Chamaerops humilis L.). Along the streams there are numerous walnut (Juglans sp.) and fig trees (Ficus sp.). According to the local people the monkeys feed in both of these, particularly during the fruiting season in late summer. Heavy falls of snow occur during some winters at least. Streams are used for irrigation and the villagers terrace the slopes to grow maize and potatoes. Even without cultivation these streams and their luxuriant vegetation, oases in a barren and unproductive landscape, would be the most likely focal points for the monkeys' activities. The macaques probably use the numerous rocky cliffs as sleeping sites rather than the low riverine trees.

2.1.2. Algeria.

Distribution. Joleaud's account (1931a) is the most comprehensive. Both he and Heim de Balsac (fig. 2.1) recorded two main locations. One in the Chiffa gorges that lie to the south of Algiers and Blida and a larger area farther to the east in the Kabylie. Joleaud gave details of specific locations in the latter area. In parts of the Kabylie, for instance to the west of Djidjelli, the mountains reach the coast and the macaques may be seen by the sea (P. Davis, personal communication). Joleaud reported that they may live to the S.E. of Stora and Davis reported seeing them above Bône. These localities are to the east of the area shown by Heim de Balsac.

Habitat. There is no detailed habitat information available. According to Joleaud they live on precipitous slopes variously covered with holm oaks, deciduous oaks and cedars. D.W. Snow (personal communication) saw them to the south of Algiers on steep hill sides covered with oak thickets and P. Davis saw them, at the locality mentioned above, in mixed cork oak (Quercus suber L.) forests on steep slopes and gullies.
2.1.3. Gibraltar.

Description. Two parties of monkeys are currently found in Gibraltar (MacRoberts and MacRoberts, 1966; MacRoberts, 1970; Burton, 1972). It is unknown whether the original Gibraltan monkeys were endemic or introduced. There were certainly monkeys there when the British took control in 1704 and since that date numerous introductions have occurred, the earliest in 1740 (Kenyon, 1938). For further details on the history and status of this population see Lydekker (1894), Forbes (1897), Hooton (1942), Zeuner (1952) and Morris and Morris (1967). The monkeys are cared for by the British Army who permit only one adult (or near adult) male per group (Burton, 1972). Since this is a highly unnatural group structure (section 2.3) some observations on these animals should be treated with caution.

Habitat. Details of climate and habitat are given by the MacRoberts’. The climate, although similar to that of the Middle Atlas in many respects, is more equable with a mean minimum January temperature of 10°C.

2.2. THE AIN KAHLA HABITAT.

The Ain Kahla forest is part of Sidi M’Guild, one of Morocco’s major cedar forests. The latter has been studied extensively by researchers from the Station de Recherches Forestières, Rabat (L’Administration des Eaux et Forêts et de la Conservation des Sols.). The Ain Kahla forestry post (long. 5° 13’w; lat. 33° 15’n.) lies at 2,010 m. In places the forest is up to 125 m. higher. Ain Leuh, the nearest village, is 22 km. by road (linear distance 12 km.) and Azrou 30 km. by road. The extent and characteristics of the study area are shown in plate 2.1.

2.2.1. Geography.

Ain Kahla lies in a dolomite-calcite region (Lepoutre, 1957-61; Pujos, 1964). The forest is found on rounded slopes broken by
PLATE 2.1(a-d). CEDAR FOREST HABITAT OF M. SYLVANUS. (a) Aerial photograph of the Ain Kahla study area. — Main study area of 5 sq. km; 1 and 2 permanent water sources (wells). Scale 3.3 cm = 1 km. Photo: Service Topographique, Rabat.
PLATE 2.1. contd.

(b) Mature cedars at Ain Kahla. These are a typical sleeping site.

continued:
PLATE 2.1. contd.

(c) Looking south across the main Ain Kahla 'bled'. The foreground shows a typical spur running down from the forest; the small bushes are chiefly Juniperus thurifera. The north facing slope in the background is sparsely clad with cedars and junipers.

(d) The Ain Kahla Forestry Post. In the foreground is a shepherds' camp.
PLATE 2.2. OAK FOREST HABITAT OF M. SYLVANUS

Oak forests (Quercus ilex) of the Middle Atlas Mountains.

(a) Near Tagounit, 10 km S.W. of Azrou.
(b) 3 km E. of Azrou on the road to Midelt.
PLATE 2.3. MIXED FOREST
HABITAT OF M.
SYLVANUS IN THE
WESTERN RIF.

Aerial photograph of Whiten's
study area at Jbel Lakraa.
Scale 3.2. cm to 1 km.
PLATE 2.4. THE OURIKA VALLEY HABITAT OF M. SYLVANUS

(a and b) Typical slopes and valleys above the village of Setti Fatma.
erosion gullies and is much dissected by lower grassland 'bleds' devoid of trees (plate 2.1a). Slopes connect the grassland with the tree line. Both in and out of the forest the ground is strewn with rocks but cliffs are small and rare. In places spurs of harder rock run down from the forest onto the bleds creating small valleys leading from the forest. These and the forest gullies are followed by tracks and paths. Owing to the porous rock there is little surface water. A stream runs from east to west through the main bled but, except during the wettest weather, never reaches the forest. Its source is a spring that gave the place its name - Ain Kahla (Black Spring). Two additional permanent water sources were found in the study area (plate 2.1a) and are important watering places for the monkeys. Both have been partially modified by the Army and shepherds to permit the storage of water and the watering of the herds. The Forestry Post of Ain Kahla lies in the centre of the main bled near to the spring and 0.5 km. from the forest. It is the only permanent dwelling in the study area. The earth track was used by vehicles carrying forest products and occasionally other vehicles. The number using it each day varied from zero during parts of the winter to probably 10-20 when there was active felling.

2.2.2 Vegetation.

Trees. The most important species are cedar and holm oak which occur either in pure stands of each species or varying mixtures. Both are exploited commercially, the cedar for timber and oak for firewood or charcoal manufacture. Mature cedars are usually 30-40 m. high but some reach 60 m. (Metro, 1958). Selective felling of cedars is practiced and regeneration is left to nature. Oak, being more sensitive to the cold (Pujos, 1964), is common on south facing slopes. In places where there has been extensive felling of oaks there are frequently dense patches of young trees. The next most common tree is Juniperus thurifera L. Since this will live in the colder parts of the forest and on areas unsuitable for cedars (Pujos, 1964) it is found primarily on the forest edge and on the spurs. These trees are grotesquely damaged by the shepherds who cut them to supplement the food for their sheep. The hawthorn (Crataegus laciniata Uoria) also grows on the
forest slopes and in places is abundant. *Juniperus oxycedrus* L. and the holly (*Ilex aquifolium* L.) are rare and found within the forest. Several other species (maple, *Acer monspessulanum* L.; yew, *Taxus baccata* L.; woody honeysuckle, *Lonicera arborea* Boiss; elderberry, *Sambucus ebulus* L.) are extremely rare at Ain Kahla but more common at lower altitude. In addition to the papers just mentioned Marion (1953-55) and Lepoutre (1957-61, 1962-63) provide further details on the biology of cedar forests.

**Herbaceous vegetation.** Except for young trees there is no shrub layer in this forest. Beneath the trees is found a herb layer of species that are almost all below 0.5 m. high and most are much shorter than this. For a discussion of the plant communities found in association with cedars and oaks the reader is referred to Negre (1952), Metro (1958) and Fujos (1964).

There are considerable differences between the herbaceous vegetation of the forest, spurs, slopes and bled. On the bled the plant cover is more or less complete. On the spur and slopes it is frequently interrupted by rocks and on the spurs by larger areas of bare rock. In parts of the forest the ground cover is complete but elsewhere the ground is covered with fallen leaves and twigs. Since the monkeys also fed outside the forest it was of interest to see if there were plant species available in these areas that were not available in the forest. A preliminary examination of this problem was made in the early summer by laying down transects across two representative parts of each habitat type and recording the presence or absence of herbaceous species along these lines. A more detailed survey would be preferable but lack of time precluded this. The results nevertheless provide a simple measure of species diversity. 79 species were recorded. After adding results from like transects the species were found to be distributed as follows:
<table>
<thead>
<tr>
<th></th>
<th>FOREST</th>
<th>SPURS</th>
<th>SLOPES AND BLED</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of species found (% of total)</td>
<td>33 (42)</td>
<td>60 (76)</td>
<td>46 (58)</td>
</tr>
<tr>
<td>No. and per cent of species in zone that were unique.</td>
<td>12 (36)</td>
<td>17 (28)</td>
<td>7 (15)</td>
</tr>
<tr>
<td>No. of species common to two or more zones.</td>
<td>4</td>
<td>22</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>17</td>
</tr>
</tbody>
</table>

The spurs had the greatest variety of plants and also the most unique species. The spurs, slopes and bled had between them 46 (58%) species that were not recorded in this sample from the forest. While there were 17 species common to all habitats the spurs, slopes and bled clearly had more in common with each other than either had with the forest. It is likely that by feeding outside the forest the monkeys were exploiting species not found beneath the trees.

2.2.3 Weather.

Ain Kahla lies in the humid/subhumid bioclimatic zone of Morocco (Metro, 1958; Sauvage, 1963). The climate is a Mediterranean one, modified by altitude; the hot, dry summers contrasting with cold, wet, snowy winters. This seasonality is important since it affects food availability. During the study my wife made regular meteorological observations. For temperature and rainfall these are supplemented by official records kept by the Ain Kahla foresters.

Rainfall. There is a mean annual rainfall of 855 mm. (table 2.1). This chiefly falls between October and March (fig. 2.4) and, as is typical for the Middle Atlas (Pujos, 1964), it tends to occur in two peaks separated by reduced falls around January. Table 2.2 gives the monthly rainfall for 1962 to 1963, and fig. 2.5 the daily rainfall for 1968 and 1969. They show that there is considerable variation between years in the quantity and distribution of the
FIGURE 2.4.
Mean monthly rainfall (1933 to 1969) and mean monthly maximum and minimum temperatures (1950 - 1954) at Ain Kahla Forestry Post. Rainfall from Pujos (1964) and table 2.2. Temperatures from Pujos (1964).
FIGURE 2.5.
Daily rainfall (including snow) for Ain Kahla Forestry Post 1968 and part of 1969. From measurements made by M. Idriess Hassan.
TABLE 2.1  ANNUAL RAINFALL AT AIN KHALA FORESTRY POST (1936 TO 1968)

<table>
<thead>
<tr>
<th>YEAR</th>
<th>mm.</th>
<th>YEAR</th>
<th>mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1936</td>
<td>1016</td>
<td>1955</td>
<td>962</td>
</tr>
<tr>
<td>39</td>
<td>836</td>
<td>63</td>
<td>1548</td>
</tr>
<tr>
<td>48</td>
<td>511</td>
<td>.65</td>
<td>966</td>
</tr>
<tr>
<td>49</td>
<td>699</td>
<td>66</td>
<td>660</td>
</tr>
<tr>
<td>52</td>
<td>595</td>
<td>68</td>
<td>973</td>
</tr>
<tr>
<td>53</td>
<td>677</td>
<td>Mean</td>
<td>855 mm. per annum.</td>
</tr>
</tbody>
</table>

Data from Pujos (1964) and meteorological records at Ain Kahlal.

TABLE 2.2  MONTHLY RAINFALL IN mm. AT AIN KHALA FORESTRY POST

<table>
<thead>
<tr>
<th></th>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1962</td>
<td>63</td>
<td>40</td>
<td>145</td>
<td>31</td>
<td>50</td>
<td>3</td>
<td>2</td>
<td>45</td>
<td>115</td>
<td>7</td>
<td>177</td>
<td>206</td>
</tr>
<tr>
<td>1963</td>
<td>64</td>
<td>101</td>
<td>136</td>
<td>107</td>
<td>78</td>
<td>8</td>
<td>2</td>
<td>6</td>
<td>130</td>
<td>31</td>
<td>27</td>
<td>11</td>
</tr>
<tr>
<td>1964</td>
<td>65</td>
<td>31</td>
<td>68</td>
<td>23</td>
<td>68</td>
<td>8</td>
<td>3</td>
<td>6</td>
<td>23</td>
<td>7</td>
<td>140</td>
<td>129</td>
</tr>
<tr>
<td>1965</td>
<td>66</td>
<td>21</td>
<td>87</td>
<td>104</td>
<td>70</td>
<td>3</td>
<td>2</td>
<td>6</td>
<td>27</td>
<td>8</td>
<td>120</td>
<td>68</td>
</tr>
<tr>
<td>1966</td>
<td>67</td>
<td>135</td>
<td>88</td>
<td>347</td>
<td>70</td>
<td>140</td>
<td>50</td>
<td>117</td>
<td>146</td>
<td>34</td>
<td>273</td>
<td>75</td>
</tr>
<tr>
<td>1967</td>
<td>68</td>
<td>130</td>
<td>23</td>
<td>106</td>
<td>42</td>
<td>40</td>
<td>21</td>
<td>34</td>
<td>4</td>
<td>53</td>
<td>84</td>
<td></td>
</tr>
<tr>
<td>1968</td>
<td>69</td>
<td>106</td>
<td>6</td>
<td>166</td>
<td>41</td>
<td>4</td>
<td>21</td>
<td>34</td>
<td>4</td>
<td>53</td>
<td>84</td>
<td></td>
</tr>
</tbody>
</table>

Data from meteorological records at Ain Kahlal. T < 0.5 mm; figures include rain and snow; blanks indicate no data available.

Pujos (1964) gives different values from some months. His figures are: Oct. '62 (126 mm), Nov. '62 (261 mm) and Jan. '63 (20 mm). The latter is known to be incorrect since a second rain gauge at Ain Kahlal (parcel 11) recorded 290 mm (Pujos, 1964).
The summer is, however, always the dryest part of the year. The months of April to November showed a pattern of two or three days with precipitation followed by longer periods of dry weather. During these months precipitation often fell as hail and was accompanied by thunder and a marked drop in temperature. Snow falls in the months of September to May but the amount of snow apparently varies greatly from year to year. From November 1, 1968 to May 30, 1969 snow fell on 39 days and lay on the ground in appreciable quantities for 82 days. On a further 19 days there was snow on north facing slopes only (excluded from this data were 11 days in March for which no data is available). Complete snow cover rarely lasted for more than a few days since snow falls were often followed by periods of prolonged low cloud and rain or by hot sun. The greatest depth of snow occurred when 43 cm. fell in two days. There was always considerable drifting and the roads from Ain Kahla were frequently impassable by vehicle. Melting of the snow caused abundant surface water and rapid erosion. Ground frosts were common during the autumn and winter (table 2.3) and dew in the summer. The autumn rain had a marked effect on the herbaceous vegetation. Over the summer this became scorched and brown; following the rain rapid new growth occurred.

Temperature. Fig. 2.4 gives the mean monthly maximum and minimum temperatures for 1950 to 1954. Owing to difficulties with apparatus we were unable to collect complete temperature records. The available data (table 2.3) shows that January and February 1969 were milder than average with mean monthly temperatures above freezing. Monthly means conceal the considerable variation that occurred during most months. From autumn through spring periods of moderate temperatures were punctuated by periods of several days of low temperature. For instance from November through January the maximum daily temperature was usually between 10 and 24°C. but five periods of near zero or subzero maximum temperatures lasting one to nine days were recorded. From autumn through spring these drops in temperature were associated with snow falls. Late in the spring these depressions decreased in magnitude and during the summer temperatures were more steady. Summer thunderstorms with hail were, however, accompanied by dramatic falls in temperature. For five months of the
### TABLE 2.3. ADDITIONAL DATA ON TEMPERATURE AND WINTER CONDITIONS AT AIN KAHLA

(a) DATA FOR 1950–1954. From Pujos (1964)

<table>
<thead>
<tr>
<th>Data Description</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean maximum temperature for the warmest month.</td>
<td>27.5°C</td>
</tr>
<tr>
<td>Mean minimum temperature for the coldest month.</td>
<td>-6.7</td>
</tr>
<tr>
<td>Mean maximum annual temperature.</td>
<td>15.7</td>
</tr>
<tr>
<td>Mean minimum annual temperature.</td>
<td>0.8</td>
</tr>
<tr>
<td>Mean of the hottest temperatures recorded during the coldest month.</td>
<td>13.4</td>
</tr>
<tr>
<td>Highest temperature recorded during the coldest month.</td>
<td>14.5</td>
</tr>
<tr>
<td>Mean of the lowest temperatures recorded during the coldest month.</td>
<td>-16.1</td>
</tr>
<tr>
<td>Lowest temperature recorded during the coldest month.</td>
<td>-18.4</td>
</tr>
<tr>
<td>Number of days with frost per annum.</td>
<td>&gt; 100 days</td>
</tr>
<tr>
<td>Number of days with snow falling per annum.</td>
<td>20 – 40</td>
</tr>
<tr>
<td>Number of days with snow on the ground per annum.</td>
<td>40 – 80</td>
</tr>
</tbody>
</table>

(b) MEAN MONTHLY TEMPERATURES DURING THE STUDY. From measurements by R. Deag.

<table>
<thead>
<tr>
<th>Month</th>
<th>Maximum Temperature</th>
<th>Minimum Temperature</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nov. 1968</td>
<td>14.9°C</td>
<td>3.7°C</td>
<td>(3 day's data missing)</td>
</tr>
<tr>
<td>Dec.</td>
<td>9.8</td>
<td>-2.2</td>
<td>(2 day's data for maxima missing)</td>
</tr>
<tr>
<td>Jan. 1969</td>
<td>12.0</td>
<td>0.2</td>
<td>(4 day's data missing)</td>
</tr>
<tr>
<td>Feb.</td>
<td>8.4</td>
<td>1.7</td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>9.5</td>
<td>2.5</td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>16.8</td>
<td>7.4</td>
<td></td>
</tr>
<tr>
<td>July</td>
<td>27.1</td>
<td>14.0</td>
<td>(10 day's data missing)</td>
</tr>
</tbody>
</table>
year the mean minimum temperature may be subzero (fig. 2.4). The
lowest temperature recorded during the study was -10°C, but temperatures
as low as -18°C have been recorded (table 2.3). Even without con-
sidering the effects of exposure and difficulties in food finding during
snowy periods (section 6.3.7) it is clear that winter conditions are
severe. The highest temperature recorded during the study was 31.5°C.

Since the above measurements were made at the forestry post it
was necessary to see whether there was any major difference between
these and the forest. For this purpose a thermometer was established
3.5 m. up a cedar tree 75 m. into the forest. It was read on 10
occasions between March and June. All temperatures were lower in
the forest. Minimum temperatures were 0.5 to 1.5°C lower but the
effect was more marked with the maximum temperatures which were 2 to
9°C lower.

Winds, cloud cover and humidity. For most of the year westerly winds
were typical. During the summer, periods of particularly hot weather
were often accompanied by more southerly winds. The extent of cloud
cover was closely correlated with rainfall. From autumn through
winter periods of prolonged overcast weather, with cloud obscuring
the tops of the trees or down to ground level, were common. Clear
periods or periods with light cloud also occurred but chiefly in the
summer. Humidity varied with rainfall, temperature and cloud cover.
In the winter the humidity was usually between 30% and >90% accord-
ing to the prevailing weather, in the summer <30% was typical. The
hot, dry season lasts from June to September (fig. 2.4). In 1968 it
was prolonged into October (fig. 2.5).

Sunrise and sunset. The sun was due south at 1220 G.M.T. Sunrise
varied between 0510 (June) and 0725 (January) and sunset between
1935 (June) and 1715 (December)*. All times are approximate since
they refer to a horizontal horizon at sea level. This gave approxi-
mately 14 hrs. 20 mins. daylight in mid-summer and 9 hrs. 45 mins. in
mid-winter. In the following chapters on behaviour this change
in available daylight hours that makes it difficult to correct a
whole day's records for seasonal differences in sunrise or sunset and
so compare accurately or add results from different times of the year.

* Based on information supplied by the Royal Observatory,
Edinburgh. See also fig. 4.15.
I have pointed out where differences in sunrise and sunset may affect the results but have not introduced a correction. All times used are G.M.T. which is the local time.

2.2.4. People and animals.

There is no cultivation in the area but the forest and bleds are traditional grazing grounds (Metro, 1958) and in the summer the semi-nomadic Berber people, with their sheep, cattle and some goats, arrived to camp on the bleds. They also have traditional rights to cut wood. Some grazing occurred on a day to day basis earlier in the year but the shepherds did not camp. Animals were grazed both on the bleds and in the forests (section 6.5.) Camps were moved in the autumn before the heavy snow falls commenced. With the arrival of the rain and snow the mud roads became difficult to use and most activities in the forest ceased until the late spring. Felling caused considerable but localized disturbance and, with the exception of a little cutting of oaks in the vicinity of well 1 in late 1968, I arranged my study area so that it excluded areas where felling occurred.

Wood cutters and charcoal burners set up camp in the forest and many of the latter remained throughout the winter. Other commercial exploitation included the collection of lichens and other plants for export. During June of each year the Royal Moroccan Army hold a two week training camp in the vicinity of well 1 and cause considerable disturbance. (This camp explains the artifacts visible in plate 4.1a).
Other animals found in the study area are mentioned in Chapter 7. In addition the following were seen in the forest; small rodents, hares, wild cats (probably Felis silvestris) and two species of snake. The forest has a varied bird life that is closely related to that of western Europe. The nomenclature used in this thesis for birds and non-primate mammals follows Etchecopar and Hue (1967) and Panouse (1957).

2.3. FACTORS INFLUENCING DISTRIBUTION.

Basic habitat requirements are, a suitable supply of food throughout the year, trees or cliffs for sleeping and escaping from predators and access to a permanent supply of water for use during dry years. The absence of permanent water may, for instance, contribute to the apparent lack of monkeys in the sparse forest to the S.E. of Ain Kahla.

2.3.1. Prehistoric factors.

Zoogeographically this species presents some interesting problems. It is unique in several ways being the only: macaque living outside Asia; macaque in Africa; non-human primate living north of the Sahara; primate other than man living in Europe today. Only one non-human primate (the Japanese macaque) lives in a more northerly position. To explain the discontinuous distribution of macaques one must recourse to fossils, comparisons with other mammals that show Afro-Asiatic connections, and speculations on past climatology and land bridges. This is too specialized a topic to be considered here at length and the reader is referred to Lydekker (1894), Trouessart (1900), Joleaud (1931a), Cabrera (1932), Heim de Balsac (1936), Zeuner (1952), Cooke (1963), Kurten (1968) and Napier (1970).

Since it is of interest to make comparisons between this species and other macaques it would be useful to discover how long the Barbary macaque has been separated from its eastern relatives. Fossil animals that have been called M. sylvanus were distributed over much of Europe
during the middle pleistocene interglacials (Zeuner 1952; Kurten, 1968). It is probably invalid, however, to give earlier European fossils different specific names and our scant knowledge of these fossils makes it difficult to pinpoint the time at which the separation into east and west macaques occurred (Delson, personal communication). Jolly (1965) considered that the pleistocene glaciations emptied Europe of its macaques and that sea barriers prevented recolonization. The most severe conditions in Southern Europe were associated with the last (Wurm) glacial 10,000 - 30,000 years ago. At that time ice covered Europe down to a line approximately from London to Prague to Dnepropetrousk (south Ukraine). There were also subsidiary ice fields in the Alps. South of the ice sheets an area of permafoot must have made the climate unsuitable for macaques over most of Europe. It is possible, however that the Iberian Peninsula, the south of France and Italy still provided suitable macaque habitats.

Why are the macaques able to survive today in northerly latitudes with harsh climates? I believe that the crucial point is their ability to fully exploit a wide variety of food resources. They obtain (often with the help of considerable manipulative skill) food from all parts of their habitat - in the trees, on and under the ground and under rocks (chapter 6). It is interesting to note the apparent ease with which Japanese monkeys pick up new skills to handle new food resources (Frisch, 1956). Their catholic feeding habits ensure that they can obtain food throughout the year in spite of seasonal differences in its availability in different parts of the habitat. In temperate regions a primate restricted to feeding in the trees on leaves and fruits would have difficulty in finding a sufficient variety of food throughout the year. The generalized structure of macaques, the compactness of their bodies with reduced extremities (e.g. tails) in some species, are probably adaptations to temperate conditions that may owe their origin to the cooler periods earlier in the Pleistocene. With the possible exception that they may be too large for such an environment, baboons might function just as well.
2.3.2. More recent factors.

There is no evidence to support Sanderson's bizarre suggestion (quoted by Tappen, 1960) that *M. sylvanus* was introduced into N. Africa during historic times. Joleaud (1931a) and Zeuner (1952) reviewed the factors that may be responsible for the species' current distribution. They concluded that man, by causing deforestation, led to the loss of the species from Europe (or its restriction to Gibraltar) and in N. Africa to its discontinuous distribution restricted to the more inaccessible areas. The monkeys have become extinct or less common in areas (e.g. the R. Kabylie) where they were used as food. Elsewhere they have been protected by totem (Joleaud, 1931a, b). Today many of the Rif populations are extremely small owing to hunting (Whiten, personal communication). Past attempts to reduce the number of monkeys in the Middle Atlas are noted in section 3.6 and discussed in the context of the forest ecology in section 6.5. Man will undoubtedly continue to play a major role in determining the distribution of the species.

2.4. SUMMARY.

The Barbary macaque lives in isolated populations scattered in mountainous areas of Morocco, Algeria and Gibraltar. Its distribution and habitats in these areas are discussed. In Morocco it is found in cedar forests and holm oak forests in the Middle Atlas, more open mixed forests in the Rif and oak and juniper scrub on steep slopes and gorges in the High Atlas.

The study area at Ain Kahla (Morocco Middle Atlas mountains) was in a cedar forest in a dolomite-calcite region. Other trees include holm oaks and junipers and there is an important herb layer but no shrub layer. More open areas on the edge of the forest have numerous herbaceous plants not found under the trees and it is suggested that monkeys feeding outside the forest were exploiting these species. There is a Mediterranean climate modified by altitude. Most of the rain (mean = 855 mm p.a.) falls
from October through March. Winters are severe with up to 4½ hours less daylight than summers, snow and minimum temperatures below freezing for up to five months of the year and down to at least -18°C.

June to September it is hot (31°C.) and dry. The forest is exploited commercially and semi-nomadic herdsmen graze cattle and sheep there during the summer.

The factors determining the distribution of the species are discussed and it is suggested that macaques can survive temperate conditions by having catholic feeding habits and a correspondingly generalized body structure. Man is probably primarily responsible for the present discontinuous distribution of the species.
3. Population Structure

3.1. Introduction.

The preliminary study (Deag and Crook, 1971) showed that the Ain Kahla forest contained numerous monkeys that moved around in parties. These parties were observed to join and split and several parties were seen to use the same wells and the same areas of forest. One aim of the population study was to analyse population structure further by determining which of these parties were basic social units or 'groups' and discovering the age-sex structure of the population. It was also necessary to discover whether the joining of parties was the union of two groups, the union of two parts of the same group, or both. The manner in which several parties used the same areas suggested a high degree of home range overlap between groups. I therefore tried to identify as many groups as possible and, by recording their movements, discover their distribution. Ideally one would like more or less simultaneous sightings for all groups. With one observer and numerous shy groups, which proved difficult to identify and follow in the forest, this was impracticable and incompatible with the other aims of the project. Instead I used the procedure of following a party and learning to recognize its members. I would then try to recognize it again and follow it on occasions over a period of several days, weeks or months. The full details of the relationship between the ranges of different groups and any seasonal changes, remains to be studied. In order to collect equivalent detail for several sympatric groups it would be necessary to concentrate upon this topic. Details of the encounters between groups are given in chapter 5.

I chose to work in the area to the north, west and south-west of the forestry post (plate 2.1), but also followed monkeys when they went out of this area. As monkeys lived in the forest continuous with the study area, the population studied was in no sense a natural unit.
3.2. DEFINITIONS OF AGE-SEX CLASSES.

To facilitate description it is convenient to divide the animals into classes based on their age, sex and some other factors such as a female's parity. The morphological and physiological criteria used to define these age-sex classes are given below and these are supported by some information on behaviour (chiefly sexual behaviour). Further information on the behaviour and spatial distribution characteristics of individuals in these classes is given in later chapters. Where ages are given they are approximate and most have been derived from the estimates given for group 6 monkeys (section 3.3.3).*

When sexing animals quickly in the field, the surest technique was to look for the testes, the callosities (in the male these form a more or less continuous shape; in the female they are separated by the genitalia), sexual swellings or long nipples. A tuft of fur on the behind, pushed up by the swelling, permitted the recognition of swollen females. While adult and subadult animals could usually be separated using these criteria, further careful observation was often necessary to separate the sexes in younger animals. My comments here are restricted to features easily noticeable in the field. Burton (1972) gave more details based on close observation of the Gibraltan animals. Note, however, that we do not always agree on the definition of age-sex classes (section 3.8.1).

Babies (B). Birth to 5-5½ months. Neonates had black fur and pink skin. They had a small tail and in the male the genitalia were visible. In their third week the two babies observed in detail developed a white triangular or diamond shaped patch of bare skin on their backs. This lasted for about one month before being covered with fur. By 4 weeks their skin had darkened to light-tan and at 5½ weeks slight changes in fur colour were recorded. By 14 weeks there were streaks of light fur along the sides of the head and back; their bellies and the inner surfaces of their limbs were almost completely light brown. The sides of the head were the last areas of fur to change. By 21 weeks one baby was completely light brown with only slight mottling and became increasingly difficult to separate, by fur colour, from infants born the year before. I therefore placed the baby - infant boundary at 5 to 5½ months and this corresponded * The age estimates given here are considered more accurate than those in Dean (1970).
to the completion of the dark to light fur change. Except for this feature the boundary between babies and infants was an arbitrary one. Development continued gradually and there was no major behavioural change at 5½ months. While initially dependent upon their mothers for food they gradually fed more and more independently. They were seen away from their mothers (at first with other individuals) from the first week of life onwards. Babies were carried ventrally and dorsally.

**Infants (I). 5 to 5½ months to 1-2 years.** Unweaned: weaning was presumed to occur when the infant was at least one year old either before or at the birth of the next sibling. Infants born in 1968 were still suckling (with no sign of ceasing) in October 1969 (section 3.3.3). Since no births were recorded from September onwards these infants must have been at least 13 months old. The evidence given in section 3.7 indicates a one or two year interval between the birth of siblings. Older infants collected a lot of food and may have received no milk from their mothers.

One infant, IF 2 (group 6), may have been orphaned at 6-8 months, indicating that they may be capable of getting all their own food at that age. In the male the penis (but usually not the testes) was visible. The now lightish-brown fur concealed the small tail. Infants were carried dorsally.

**Juveniles (J). 1 or 2 years to 3½ (females) or 5 (males).** Weaned animals that had the same colour fur as infants. In 3-4 year old males the small testes in the grey blue scrotum were clearly visible. Juvenile males did not engage in full sexual behaviour. Their canines were not erupted below the occlusal plane. In females less than 3 years old no sexual swellings were observed. At approximately 3 years of age (May-June) they developed small pink swellings of the skin around the anus and a slight swelling of the skin beneath the genitalia. Although extremely small these swellings inflated and deflated just like those of older females. At about 3½ years of age (January) the swellings increased in size and the female was then recognized as subadult. Juveniles were not carried. The older juvenile males were as large as small adult females and subadult females.
Subadult females (SF). 3½ to 5 years (possibly up to 6 years if their first conception failed). Nulliparous females with small button like nipples hidden in their fur. It is unlikely that such animals could be distinguished from 5-6 year old females whose first pregnancy failed by abortion or death of the baby soon after birth. (Burton, 1972 noted that on Gibraltar some females either failed to conceive or carry until 6 years old). The sexual swellings of these females (around the anus) were much larger than those of juvenile females. They were bright pink with only occasional traces of blue-grey. The subgenital skin was brownish and slightly swollen. These swellings were continuations of those developed during the previous year (see juvenile females) and they continued to inflate and deflate for many months before the copulation season. At the start of the copulation season maximal swellings (comparable in size with those of adult females) developed. The lips of the vulva also swelled and were coloured white, pink or brown. The skin beneath the genitalia also reached maximal swelling and was coloured pink or brown. Compared with adult females, they were hesitant in their sexual approaches to adult males at the start of the copulation season. They had the light brown fur of juveniles and infants, or tended towards the colour of adult females.

Subadult males (SM). 5 to 7 years. Smaller and not as heavy as adult males. They had shorter fur on the body and less fur around the neck. The fur shade varied from the lighter brown of juveniles to the darker, richer, slightly olive, brown of the adult. The canines were erupting below the occlusal plane. The descended testes were large but not as large as those of adult males. The scrotum was pink. They engaged in full sexual behaviour.

Adult females (AF). 5+ (or in some circumstances 6+) years. Females that had given birth: These were usually the same size as, or larger than, subadult females and the larger animals were similar in size to subadult males. Details of pelage shade and markings varied from individual to individual. A few were the light, juvenile brown, most were a richer, darker brown and still others almost ginger. Many had small patches of black fur on their beard, back or limbs. Some that
appeared older than average were quite grey and had white patches on their limbs. Adult females usually had longer fur on the body and more fur around the face than subadult females. When suckling young they had long, pendulant nipples that clearly distinguished them from subadults. In contrast to subadults the sexual swelling around the anus was blue-grey with only the occasional patches of pink. In some females (probably those who were not suckling) the skin above the anus never completely receded. The skin was also clearly visible for some months following birth. Adult females with no unweaned offspring (and which had presumably either not conceived the previous year or had lost their baby) and those suckling infants (not babies) had slightly swollen, incomplete swellings from July onwards. At the start of the copulation season maximal swellings developed. As with subadult females these included a swelling of the lips of the vulva (dark blue-grey or slightly white) and some swelling beneath the genitalia. The latter was difficult to see in adults. Sexually receptive females suckling infants, continued to do so during at least the first part of the copulation season.

**Adult males (AM). 7+ years.** The largest animals with completely eruped canines: According to Burton (1972, quoting Holmes) they may weigh 27-33 kgs. (60-70 lbs), but Didier and Rode (1936) give the weight of adults (sex not recorded) as 5-10 kg. and Napier and Napier (1967) recorded 11 kg. for one adult male. They participated in full sexual behaviour and had large testes and a pink, sometimes furry, scrotum. The fur on the body and especially around the neck was long. As with adult females there were various pelage shades and markings; the youngest males had rich brown (sometimes olive-brown) fur and the oldest had grey-brown fur. Between these extremes various combinations were seen. Comparison between males seemed to indicate a gradual increase in grey (with age) from the back of the animal forwards.

### 3.3. GROUP COMPOSITION.

#### 3.3.1. Methods and terminology.

During the preliminary study the grouping tendencies of the monkeys were difficult to establish owing to the shyness of the
animals, the forested habitat and the high frequency with which parties met and moved in close proximity (Deag and Crook, 1971). Caution was therefore required before calling a party of monkeys a 'group'. The term 'group' is reserved for the basic social units of a species, where their composition is known to be more constant than a casual association of individuals (Crook, 1970; Struhsaker, 1969). The term 'party' is used for associations of monkeys of unknown affinity, composition or size limit. As a working definition, I upgraded parties to group status if the party was not subsequently seen to divide into smaller units and if either the party was followed during at least three consecutive days during which a complete count was obtained, or if I could identify some individuals in the party after at least a day's break in the observation.

It was necessary to establish these criteria to distinguish groups from the numerous unidentified parties present throughout the study. Recognition of groups would have been considerably easier if groups had repeatedly used the same sleeping trees or if they had had less home range overlap. The problem remained that some groups, recognizable at the start of the population study, were unrecognizable at the end of the study. This was primarily due to the difficulty of recognizing individuals. With the possible exception of groups 12 and 13 (that may have been numbered earlier in the study) it is thought unlikely that a group was numbered twice. Individuals whose identification was based on physical defects such as a broken finger or bad limp could be repeatedly recognized. Less permanent and less unique features, such as differences in fur colour, scars and the fur patterns produced during molting were not reliable. The effect of rain or wind on the fur made it difficult to recognize individuals and the effect of the molting was catastrophic. During the population study I generally found it impossible to recognize individuals by their facial features unless they were already in an identified group. Individuals within a group could also be separated by the patterning of blue pigment on the pink skin of their flanks, posterior to the armpit and anterior to the groin. This was particularly useful for separating molting individuals, since these marks were most clearly visible at that time. On a day to day basis, differences in sexual swellings were also used. Records were kept of monkeys that had features suitable for individual recognition.
Two techniques were used to count the monkeys and to record the numbers in each age-sex class. A complete count was only possible on rare occasions when the animals moved across an open space or track. (Occasionally their tracks in the snow also permitted an accurate count). At other times repeated sample counts were made by recording, at intervals, those visible or known (by some other criteria) to be present at the time of the count. Unclassifiable individuals were recorded as "others". The minimum number of animals in the party or group could then be found by summing the maximum numbers known to be present (over the period of observation) in each age-sex class (Aldrich-Blake, 1970). Unless party or group size is known, sample counts may tend to underestimate the age-sex class containing the largest number of individuals. This is because there is a smaller chance of them all appearing in a sample count of small size. Sample counts also assume that all age-sex classes are equally visible. To reconstruct party or group size from sample counts one must either be able to recognize most of the individuals or at least be confident that party or group size is constant and not temporarily swollen by associations with other groups. For instance, on several occasions a series of sample counts added up to more individuals than there were known to be in a group. In some cases, subsequent observation revealed that the counts had been made when, unknown to the observer, two groups were in close proximity to one another.

3.3.2. Size of groups.

The animals lived in social groups that contained several adult males as well as a full cross-section of other age-sex classes. * Table 3.1a gives the composition of five groups and one party (which was counted repeatedly and whose size and movements indicated that it

* 'Multimale groups' as defined by Eisenberg et al (1972). There is at present no suggestion of habitat related differences in group composition in this species. In the Ourika Valley J.H. Crook and I counted a party that included two or three adult males (Deag and Crook, 1971). Multimale groups also occur in the Middle Atlas oak forests and in the Rif (Whiten, 1972, see also this chapter section 3.8.2).
was almost certainly a group). These compositions were based on complete and sample counts in which all the individuals were repeatedly identified. Since small groups and groups observed for a long time were likely to provide more opportunity for complete counts than larger groups, the mean size of the group in table 3.1a will be a biased estimate of the population mean. Table 3.1b records the known details for other identified groups. Considered with the previous subtable this shows that groups ranged in size from 12 to at least 36 individuals with a mean group size of 24.

Table 3.1c records complete counts for six parties. The totals here are known to be accurate but since the parties were not repeatedly followed the identifications of age-sex classes could not be checked. The behaviour and size of these parties would suggest that they were 'groups'. Larger parties (for instance, 51, 57, 59, 69, 71, individuals), were also recorded. Experience showed that parties of this size involved at least two groups in an encounter. This could be deduced both from the occurrence of recognized groups within some of these parties and also by their movements (see chapter 5).

During the single group study there were no changes (except a birth) in the size and composition of group 6. This confirmed that the groups have a reasonably constant composition. (Detailed observations ceased, however, during the early mating season when movement between groups is known for some male macaques (Lindburg, 1969).) In the population study only one animal (an adult male) was known to have left a group. He may have been seen subsequently in a neighbouring group but there was no opportunity to confirm this.

3.3.3. Composition of groups.

Table 3.1a gives, for the most accurate counts, the percentage of each age-sex class present. On the basis of the corresponding data it is possible to calculate the following ratios:
The following counts were made at various times of the year. As a consequence, the lack of babies in some groups will be due to the offspring of the last birth season being too old for inclusion in the baby category.

(a) Complete counts. 5 identified groups and one party.

<table>
<thead>
<tr>
<th>GROUP NUMBER</th>
<th>AM</th>
<th>SM</th>
<th>AF</th>
<th>SF</th>
<th>J</th>
<th>I</th>
<th>B</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Party**</td>
<td>2</td>
<td>0</td>
<td>5</td>
<td>*</td>
<td>3</td>
<td>1M+3</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>7</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>0</td>
<td>2M</td>
<td>2F+2</td>
<td>0</td>
<td>15</td>
</tr>
<tr>
<td>8</td>
<td>3</td>
<td>1</td>
<td>4</td>
<td>*</td>
<td>1M+1F</td>
<td>1F+1</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>3</td>
<td>4</td>
<td>3</td>
<td>6</td>
<td>*</td>
<td>2M+1F</td>
<td>2M+2F+3</td>
<td>0</td>
<td>23</td>
</tr>
<tr>
<td>10</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>1</td>
<td>3M+2F</td>
<td>1M+1F+3</td>
<td>0</td>
<td>21</td>
</tr>
<tr>
<td>6***</td>
<td>3</td>
<td>2</td>
<td>6</td>
<td>3</td>
<td>3M+3F</td>
<td>1M+2F</td>
<td>1M+1F</td>
<td>25</td>
</tr>
<tr>
<td>TOTAL</td>
<td>16</td>
<td>11</td>
<td>31</td>
<td>25</td>
<td></td>
<td></td>
<td>27</td>
<td>110</td>
</tr>
<tr>
<td>%</td>
<td>14.5</td>
<td>10</td>
<td>28</td>
<td>23</td>
<td></td>
<td></td>
<td>24.5</td>
<td>100</td>
</tr>
</tbody>
</table>

* Subadult females not separated from juvenile females in these counts. *** Composition at end of single group study. ** 23.12.68.

(b) The known details for other identified groups. (Based on sample counts). **

<table>
<thead>
<tr>
<th></th>
<th>OTHERS</th>
<th>TOTAL++</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>3</td>
<td>35</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>29</td>
</tr>
<tr>
<td>5</td>
<td>1M+3</td>
<td>36</td>
</tr>
<tr>
<td>11</td>
<td>0</td>
<td>29</td>
</tr>
<tr>
<td>TOTAL</td>
<td>41</td>
<td>129</td>
</tr>
</tbody>
</table>

* Subadult females not separated from juvenile females in these counts.
** Counts are not available for the remaining identified groups. Estimates are as follows: group 1 (at least 30); group 9 (> 25); group 12 (ca25); group 13 (unknown). These were excluded from the estimate of mean group size.
++ These totals are probably quite close to the real figures. They were based on several sample counts over a period of several days or weeks.
TABLE 3.1. continued.

(c) Complete counts - parties.

<table>
<thead>
<tr>
<th>DATE</th>
<th>AM</th>
<th>SM</th>
<th>AF</th>
<th>SF</th>
<th>J</th>
<th>I</th>
<th>B</th>
<th>OTHERS</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.8.68++</td>
<td>6</td>
<td>1</td>
<td>7</td>
<td>*</td>
<td>3</td>
<td>1</td>
<td>4</td>
<td>0</td>
<td>22</td>
</tr>
<tr>
<td>2.8.68++</td>
<td>4</td>
<td>0</td>
<td>6</td>
<td>*</td>
<td>2</td>
<td>5</td>
<td>3</td>
<td>0</td>
<td>20</td>
</tr>
<tr>
<td>22.12.68</td>
<td>5</td>
<td>2</td>
<td>8</td>
<td>*</td>
<td>(4M+2F+6)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>27</td>
</tr>
<tr>
<td>25.12.68</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>*</td>
<td>1M+1F</td>
<td>4</td>
<td>2</td>
<td>3 or 4</td>
<td>19 or 20</td>
</tr>
<tr>
<td>28.12.68</td>
<td>6</td>
<td>6</td>
<td>11</td>
<td>*</td>
<td>1M+6</td>
<td>9</td>
<td>0</td>
<td>0</td>
<td>39</td>
</tr>
<tr>
<td>30.12.68</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>19</td>
</tr>
</tbody>
</table>

*Subadult females not separated from juvenile females in these counts.

** Accurate totals but repeated checking of identifications not possible.

++ Counts made with J.H. Crook during the preliminary study.

+Infants counted with juveniles.
Ratios - based on table 3.1a

<table>
<thead>
<tr>
<th>Ratio Description</th>
<th>Overall</th>
<th>Highest*</th>
<th>Lowest*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult and subadult males: adult females (27:31)</td>
<td>1:1.1</td>
<td>1:2.5</td>
<td>1:0.9</td>
</tr>
<tr>
<td>Adult male: adult female (16:31)</td>
<td>1:1.9</td>
<td>1:2.5</td>
<td>1:1.3</td>
</tr>
<tr>
<td>Adult males and females and subadult males: subadult females, juveniles, infants and babies (58:52)</td>
<td>1:0.9</td>
<td>1:1.3</td>
<td>1:0.5</td>
</tr>
<tr>
<td>Adult females: infants and babies (31:27)</td>
<td>1:0.9</td>
<td>1:1.2</td>
<td>1:0.5</td>
</tr>
<tr>
<td>Subadult females and juveniles: infants and babies (25:27)</td>
<td>1:1.1</td>
<td>1:2.3</td>
<td>1:0.5</td>
</tr>
</tbody>
</table>

* The highest (or lowest) ratio found in any single group on table 3.1a.

In this sample there were therefore almost two adult females to each adult male. A more correct comparison of equivalent aged animals is made by including subadult males. The ratio is then closer to unity. The remaining ratios are discussed in section 3.6.

The composition of group 6. Since the behaviour of individuals in group 6 is discussed in subsequent chapters details of its composition are given here. At the start of the single group study the group contained 24 individuals. One was BF 1, born a day or so before the single group study began. Another baby, BM 2, was born shortly afterwards giving a total of 25. On 15.12.68, an adult female was found dead in the snow on a route taken by group 6. The absence of tracks from any other group indicated that the female must have come from group 6. During the single group study one of the three infants was without a mother in the group, (the remaining two, of approximately the same age, were still suckling) and the dead female was possibly this infant's mother.

At the end of the single group study the group contained the following: 9 adults (3 M, 6 F), 5 subadults (2 M, 3 F), 6 juveniles (3 M, 3 F), 3 infants (1 M, 2 F) and 2 babies (1 M, 1 F). Details of individuals are given below and on table 3.2. Where ages are given, these are estimates. Since there was a definite birth season**age-related size groups could be seen in the younger animals; after four years or so, such judgements were more difficult. The letters and numbers used to identify individuals record their age-sex class and (with the exception of babies) their social rank in

** See section 3.7.
### TABLE 3.2

**REFERENCES TO BIRTH SEASONS OF GROUP 6 MONKEYS**

<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>EM2</td>
<td>IM1</td>
<td>JM3</td>
<td>JM2</td>
<td>JM1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SM1</td>
<td>AM1</td>
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<td>SM2</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>AM2</td>
</tr>
<tr>
<td>Females</td>
<td>BF1</td>
<td>IF2</td>
<td>JF3</td>
<td>JF1</td>
<td>SF1</td>
</tr>
<tr>
<td></td>
<td>IF3</td>
<td>JF2</td>
<td>SP2</td>
<td>SP3</td>
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</tr>
<tr>
<td>Age(Years)*</td>
<td>&lt; 1/2</td>
<td>1-1 1/2</td>
<td>2-2 1/2</td>
<td>3-3 1/2</td>
<td>4-4 1/2</td>
</tr>
</tbody>
</table>

* At end of project.

** For these and older animals birth seasons and ages are estimates.
their age-sex class, or (infants) their age class. The criteria for ranking are given in chapter 10. Only one individual changed age-sex class during the single group study (see below).

Notes on the monkeys in group 6. (See also table 3.2). Details of sexual swellings have not been given below since the details available for these animals have been incorporated into the general descriptions given in section 3.2.

BF 1 Estimated date of birth, 11.5.69 (see chapter 11) Mother was AF 2.
EM 2 Estimated date of birth, 23.6.69 (see chapter 11) Mother was AF 4.
IM 1 Mother was AF 1) still suckling at the end of the study. No
IF 3 Mother was AF 3) indication that they were about to stop.
IF 2 Mother assumed to be adult female found dead on 15.12.68.
JF 3 No sexual swelling during the whole of the single group study.
JM 3 Testes not noticeable.
JF 2
JF 1 small pink sexual swellings. Did not copulate.
JM 2 Testes descended but small.
JM 1 Testes descended. Canines not erupted below the occlusal plane.
Approached females in oestrus but did not participate in full sexual behaviour.
SF 1 Had pink sexual swellings and copulated in Sept./Oct. 1969.*
SF 2 If pregnant they would have given birth in 1970.
SM 1 Engaged in full sexual behaviour. SM 2 was probably younger than SM 1.
SM 2
AF 2 Mother of BF 1. Suckling and anoestrous at end of the study.
AF 4 Mother of EM 2. (Theoretically subadult at the start of the single group study). Primiparous, before the birth of EM 2 she had short nipples and did not associate with an infant. Suckling and anoestrous at the end of the study.
AF 6 A crippled female that walked in a half crouched position with her behind close to the ground and one leg permanently flexed under her body. The other leg was partially flexed but straightened when she ran. Nevertheless she kept up with the group without difficulty. Could not maintain the presenting posture during copulation and hence the male either kept

* In fact SF3 was not seen to copulate but it is assumed that she would have been seen to do so had observation continued (see p469).
kept one or both hind legs on the ground or did not complete the copulation. This malformation probably prevented her, for one reason or another, from bearing young. Had no unweaned young. Copulated Sept./Oct. 1969.

AM 1 Males in their prime.
AM 2 Males in their prime.
AM 3 Probably the oldest male.

3.4. THE DISTRIBUTION OF GROUPS.

3.4.1. Methods.

When a group or party was located the estimated position of its centre (and occasionally the position of outlying animals) was recorded on a map of the study area. Complete or incomplete day journeys (section 4.2.1) were also plotted. One map was used for each day. The map was prepared by enlarging, by hand, aerial photographs, *(Plate 2.1) with a scale of 1:25,000. It was not possible to check the accuracy of the photographs with measured distances on the ground but a check with a map of the area ** showed that the two were in close agreement. The map prepared for field use had a scale of 1:10560 (9.5 cm. to 1 km. or 6" to 1 mile). Checks between the completed maps and the original photographs showed that most distances were within ± 4% -- a negligible amount since actual distances in the field had to be measured by pacing or by eye.

When the field work was complete the map was divided into quadrats of approximately 1 hectare (100 x 100 m.) and the movement of groups in relation to these quadrats was used to analyse home range phenomena. In studying the spatial distributions of objects or animals the size of the quadrats selected can have a marked influence upon the results obtained (chapter 13). Selection of large quadrats would lead to an increase in apparent home range size. A smaller size would lead to too fine a measurement, unwarranted accuracy and a smaller home range

* Provided by the Ministère de l'Agriculture, Service Topographique, Rabat.

** 1:100,000 Sheet N-1-30 VII-2 (Azrou) Published by Ministère des Travaux Publics et des Transports, Institute Geographic National, Paris, and supplied by the Ministère de l'Agriculture, Service Topographique, Rabat.
size. To balance these effects hectare quadrats were selected since they approximated to the size of the area occupied by the foraging group.

Home range is defined here as the area used by a monkey group during a specified period of time. Unless animals are followed for 100% of the time the known extent of home range is only an estimate of the actual range. The accuracy of this estimate will depend upon the proportion of the time period the animals were followed, the frequency with which they used different areas and so on. For a more detailed discussion of home range see Jewell (1966). The known extent of a group's home range was determined by recording which quadrats the group was seen in; quadrats surrounded, but not actually seen to be used, were also included in calculations of home range size. It might be argued that a more exact measurement of home range size would be obtained by recording the actual positions of animals. Since it was often impossible to see all of the outlying members of a group nothing would be gained by such a method.

3.4.2. Results.

The known extent of home ranges for the groups identified in the population study are recorded on fig. 3.1. (It has, for clarity been necessary to smooth the outlines of the ranges and to divide the ranges between two figures. The reader should imagine them superimposed). Group 1, identified during the preliminary study, (with J.H. Crook) and in the early part of the population study used the N.W. part of the study area. The groups were observed for unequal periods of time and the ranges do not represent complete home ranges of the groups during the population study. Later observations with group 6 showed that only after ca. 370 hrs. of observation did the group infrequently enter squares in which they had not been previously seen (fig. 3.4). A first examination of fig. 3.1 indicates that during the population study there was a high degree of home range overlap with several groups using the same area.

It is important, however, to show that the overlap of ranges is not an artifact due to the groups using exclusive, but shifting,
The known extent of home ranges during the population study. The numerous groups using the same ground made it necessary to plot half of the home ranges on a separate map (fig. 3.1b overleaf). The reader should imagine this superimposed on fig. 3.1a. (— edge of forest; — tracks).
FIG. 3.1 (b) - see fig. 3.1a.
areas. This was clearly not the case since on any one day or during any one week identified groups were seen moving over the same ground. This is also shown by fig. 3.1a where it can be seen that: (a) group 5, observed immediately after group 2, had considerable overlap with the latter. (b) groups 5 and 6, observed during the same period, had considerable overlap. (c) groups 5 and 6 also had overlap (less than with each other) with party 2. These findings are confirmed by fig. 3.1b and by the single group study, fig. 3.3.

The population study covered several changes of season and was known to include, for group 6 at least, a change in the area used.

A shift in group 6's home range. Fig. 3.2 shows the area used by group 6 during six observation periods. Previous to 20.11.68 group 6 used an area to the north and west of the main bled (3.2a). After this the group was only observed on the northern side of the bled (fig. 3.2b-f). This shift in range was, I believe, a withdrawal into the groups 'main' home range, the excursions to the south having been movements induced by water shortage during the summer and autumn of 1968. A dry, early summer was followed by a dry, late summer and early autumn. From August 24th to November 1st only ca. 4 mm. of rain fell (fig. 2.5). During our preliminary study and in the early population study the area of forest to the west of the bled was used by many groups moving north or south en route to or from well 1. It is possible that group 6 (which was never actually seen visiting well 1) also made these movements and that its range in early November was the remnant of such a modified ranging pattern. During 1969 the group obtained its water in its 'main range' but on several occasions the water holes were dry or almost dry and only filled by a fortuitous rain or hail fall (chapter 6). Fig. 2.5 shows that there was more rainfall in July, September and early October 1969 than in the equivalent period of 1968, and it seems likely that the need to move to permanent water sources will vary from year to year. (Ideally it is also necessary to compare temperature and rate of evaporation). Presumably these movements would be restricted to groups with no permanent supply of water in their home range.
FIGURE 3.2.
The known extent of group 6's home range during six observation periods.
A. 08.11.68 to 20.11.68 occupancy hours = 45.
B. 24.11.68 to 13.02.69, 58 hours.
C. 13.05.69 to 08.06.69, 233 hours.
D. 30.06.69 to 21.07.69, 188 hours.
E. 11.08.69 to 26.08.69, 112 hours.
F. 27.08.69 to 06.10.69, 191 hours.

The and symbols indicate the position of hectares 12, 18 and 12, 37 respectively.
Alternative explanations are possible; for instance a change in the composition of the group in late November 1968 may have resulted in different animals controlling the group movements. Water dependent changes in range utilization have been reported for other primates. Altmann and Altmann (1970) found that in the dry season baboons, *Papio cynocephalus*, the home range of one group was limited to the vicinity of a water hole. Their dry season range was, however, contained entirely within the large wet season range. They also reported a possible difference between years that was apparently dependent upon differences in rainfall and evaporation.

Fig. 3.2 (c to f) shows that there was subsequently no major change in the area used by group 6. The differences between the figures are probably due to chance. The sum of these figures (c to f) was used to define group 6's home range for the single group study (Fig. 3.3). From now on I shall refer to this area as group 6's home range. It was 1.17 sq. km. - including 2 hectares surrounded but not seen to be used. Fig. 3.4 gives (for the single group study) the cumulative area occupied, plotted against occupancy hours. The steep rise of this curve indicates that initially the group frequently entered 'new areas'. By 370 hrs. over 95% of the known home range had been entered and the rate of entry into new areas fell rapidly. It can therefore be concluded that group 6's known home range for this period corresponded closely to its complete home range for the period.

At least three other groups and parties used group 6's home range (fig. 3.3). The ranges of groups 12 and 13 were plotted by linking together hectares in which they were each seen. Time did not permit the following of these other groups in order to determine their complete home range. The area of overlap is therefore smaller than in reality. A party (known not to be either group 6, 12 or 13) was located twice in the area of overlap of the other three groups. The evidence presented here clearly confirms that there was extensive home range overlap with no group having exclusive use of an area. It is shown in section 4.3.2 that group 6 did not spend an equal amount of time in all parts of its home range. 36% of the home range accounted for 75% of the entries to quadrats. It is unknown whether other groups had similar core areas. Three points suggested that they
The known extent of group 6's home range during the single group study and its overlap with other groups.

N.B. As observations were concentrated upon group 6, the range of the other groups (and hence their total overlap with group 6's range) is incompletely known. A party (not group 6, 12 or 13) was also seen in group 6's range.
FIGURE 3.4.
The cumulative area occupied by group 6 (during the single group study) plotted against quadrat occupancy time. The area plotted does not include 2 hectares surrounded but not seen to be used. (Quadrat occupancy time is defined on p. 66.)
did and that these areas possibly did not overlap extensively: Other groups neither visited nor slept in group 6's core area with the frequency one would expect if it had been included in their own core area; the location of encounters between group 6 and other groups was approximately correlated with the edge of group 6's core area (section 5.5). The relationship between groups living in the same area is discussed further (section 5.5) after the intergroup encounters have been analysed.

3.5. ESTIMATION OF POPULATION DENSITY.

The limits of the study area are plotted on plate 2.1. It is impossible to state exactly how many groups used this area, and therefore difficult to give an accurate estimate of population density. Within the study area there was a minimum of 13 groups. This is based on the 11 groups known from the population study plus the two parties whose ranges were included in fig. 3.1a. (Groups 12 and 13 have been excluded since I cannot be absolutely sure that they were not numbered earlier in the population study.) Groups that probably lived primarily outside the study area were also known to enter it and, as mentioned above, a number of unidentified parties could always be found. The entry of these parties was probably most frequent in the vicinity of the wells. With two exceptions the study area included the known home range for all the groups and parties plotted on fig. 3.1. Group 1 also entered the area to the N.W. of the study area and party 1 was seen to enter the area to the S.E. of the study area. Since known home ranges did not correspond to complete home ranges, it is possible that other groups did the same. In calculating population density it has been assumed that use of the study area by unidentified groups will be balanced by use of areas outside the study area by the identified groups.

Two methods are used here to estimate population density. Because of the above assumptions (and those included in the methods) it must be emphasized that the results are estimates and not absolute figures. The 13 groups found within the study area contained about 350 monkeys (based on table 3.1 (a and b), plus group 1...
(ca 30), group 9 (>25) and party 1 (59 minimum)). Since the study area was 5 sq. km. this gives an estimate of 70 per sq. km. (b) Group 6 had a 75% frequency area of 0.42 sq. km. (section 3.3.2). If it is assumed that all groups had these areas, that the size of the area was proportional to group size, and that the 75% areas did not overlap extensively with each other, this gives an estimate of 25/0.42 = approximately 60 per sq. km.

Population density appears to have been of the order of 60 - 70 per sq. km. While the accuracy of this estimate is unknown it seems to be of the correct order of magnitude. For instance, group 6's home range of 1.17 sq. km. was used by a minimum of three other groups that also used parts of the surrounding forest.

3.6. HEALTH, MORTALITY AND MOULTING.

Health. The monkeys almost always gave the impression of good health, but ailments such as coughs, sneezing, hiccuping and vomiting were, however, recorded. One animal coughed persistently enough for this to be useful in group identification. Injuries or malformations were relatively rare. They included a broken little finger, a permanent limp with a hind leg, a female with malfunctioning hind legs (see 3.3.3) and a subadult male with a humped back. None of these prevented the animals from keeping up with their group. Several animals were seen with scars or places where fur had apparently been pulled out. During some seasons, however, patches caused by moulting could be easily mistaken for scars. Only one fresh wound was seen; a subadult female had a cut on her sexual swelling. This reflects the low incidence of physical damage during fights.

Mortality. Only one 'natural' death was recorded. An adult female was found dead during a snowy period (see 3.3.3). Marks in the snow indicated that it had either fallen from a tree dead, or died on the ground. The only non-monkey foot prints in the snow were of scavenging ravens (Corvus corax) and there was no reason to suspect that it was killed by a mammalian predator. No monkeys were known to be caught by non-human predators (chapter 7). Times of drought and
severe winters with low temperatures, iced trees and snow covered
ground are probably periods of stress. During the winter, however,
the moist conditions permit the monkeys to exploit cedar leaves, an
additional (and probably less preferred) source of food (chapter 6).

If there was an approximately constant birth rate and no post
natal loss one would expect to find a subadult female and juvenile:
infant and baby ratio of 3:2 or 1:0.7. The overall observed ratio
was 1:1.1 (section 3.3.3) probably indicating mortality between the
baby and adult stages. In practice one would expect mortality
both before, during and after this stage but with the present data
it is not possible to measure it. The adult and subadult male:
adult female ratio of 1:1.1 shows that (if one assumes a 1:1 ratio
at birth) there was no significant difference in the mortality of the
sexes.

Losses due to people either killing or capturing monkeys, have
probably largely replaced other forms of predation. At Ain Kahla
we were told of monkeys being shot, because of the damage caused by
their removal of cedar bark. This apparently occurred around 1955
when monkeys were shot throughout the Middle Atlas. One report
indicated that ca 50 monkeys may have been caught at Well 1 during
1967. These monkeys and several hundred others caught previous to
1968 in other parts of Morocco were used for virological research
at the Institute Pasteur, Casablanca. During the study at least
10 monkeys (mostly young) were caught or shot in or near the study
area by soldiers, shepherds and foresters. In 1969 about 120 were
captured near Azrou for export to France. Captive animals were seen
in several villages and shooting of monkeys is known to occur in the
High Atlas and the Rif (Whiten, personal communication). There is
at present no indication of trapping on the scale seen in India
(Southwick et al, 1970), but this might easily happen if M. mulatta
become more difficult to obtain. I believe that an official permit
is necessary to take monkeys from the forest, with an annual maxi-
mum authorization of 100 animals. It is unknown whether such a
limit is enforced. (See also the discussion in section 6.5).

Moulting. The animals moulted from late January onwards. After
that time individuals with numerous bare, pink patches could be seen
as the result of hair loss. These patches were gradually covered by a new growth of short dark fur that did not reach full length for some months. There was a considerable spread in moulting, with monkeys still with bald patches in August. Adult males seemed prominent amongst the early moulters. In group 6, juveniles and infants moulted later than other age-sex classes. On 30.6.69 and 1.7.69 I recorded whether or not the individuals had moulted. Those that had either started or finished moulting were 7 adults (2 M, 5 F), 4 subadults (2 M, 2 F) and a juvenile male. Those that had not started to moult were 4 juveniles (2 M, 2 F), 3 infants, 2 babies and an adult female. Details were not recorded for three monkeys. (See plate 3-I)

There are interesting similarities with the timing of moulting in *M. mulatta* on Cayo Santiago and La Parguera. Vessey and Morrison (1970) found that the moult commenced at the end of the mating season; starting about December/January on Cayo Santiago and April on La Parguera. They suggested that the onset of moulting resulted from a decrease in sex hormones. The data from this study therefore supports their hypothesis. If there is a close link between moult and falling testosterone levels this may be one of several factors determining the copulation season. In this population with severe winter temperatures the long coat is presumably protective. Selection would therefore favour a mating season late in the year. Testosterone would be high in the winter months and hair loss prevented until the worst of the winter had passed. Vessey and Morrison found that moult extended beyond the birth season and also found that adult males were early moulters and prepubetal monkeys among the last to moult.

3.7. Mating and Birth Seasons; Birth Interval.

Mating Season. Copulations were seen during the autumn and winter. Unfortunately I was unavoidably absent from the study area during parts of the autumn in both years. The available data confirms, however, that the distribution of copulations is more or less similar to the Gibraltan animals (MacRoberts and MacRoberts, 1966).
PLATE 3.1 (a – c).

MOULTING

(a) and (c) Adult males growing new fur after moulting (3.6.69).

(b) The same animal as in (a) with fur growth completed (28.9.69). ((a & b), AN3, group 6).
In 1968 I was at Ain Kahla until 9.10.68. Up to that time no complete sexual swellings were seen and only incomplete sexual behaviour (e.g. presentations and inspection of anogenital area by males followed by females grooming the male) were seen during observations on several groups. I returned on 30.10.68. By the second week of November complete swellings were seen and subsequently consort behaviour with full copulations and copulation calls. I believe that this was the true start of the copulation season and that it had not started during my absence. Copulations were seen from November to January. From February, sexual behaviour became less intense and gradually decreased until by April it had returned to the level of early October. During the rest of 1969 no sexual behaviour of note was seen until early September. There was then a noticeable increase in sexual activities. Males approached females more frequently and this was followed by presentation and close inspection of the anogenital area by the male. Interestingly there also seemed to be an increase in presentation by females to males in 'non-sexual' situations. At other times of the year, females passively avoiding a moving male usually walked away; they now stood and presented. When I returned to the study area in late September consort behaviour with copulation and ejaculation was in progress and was observed until the termination of the study. Between early and late September there was a marked change in the sexual swellings. Subadult females (that had cycling swellings throughout the summer), adult females that were suckling infants, and adult females with no unweaned offspring had all developed maximal swellings. A seasonal change in spermatogenesis is known for rhesus males (Conaway and Sade, 1965) and is probably present in all macaques that have distinct copulation seasons. A seasonal change in female receptivity, that is independent of the cessation of lactation, is also suggested by the present study. Two of the three types of female listed above were definitely not lactating in the months preceding sexual activity. During that time they had cycling, incomplete, sexual swellings and made no sexual advances to males. The presence of complete swellings corresponded to an increase in sexual invitations by the females. It is possible that the onset of sexual activity in the female is stimulated by the investigatory
activities of the male but I consider this unlikely and propose that both male and female reproductive activity are facilitated by particular environmental stimuli. Hartman (1931) found evidence for a period of lowered fertility, due to cessation of ovulation, in rhesus monkeys. This period corresponded to the season when the males, although apparently still fertile, were less sexually active. *

MacRoberts and MacRoberts (1966) reported a mating season on Gibraltar from mid October to April with fertile copulations between November and March. The start of the 1968 mating season at Ain Kahla fell within that period but in 1969 it was earlier. Whiten, (1972) observing a population in the Rif in 1971, first saw mountings on approximately October 28th. These continued during the following month. The MacRoberts' considered that the onset of copulations was stimulated by decreasing day length and/or daily temperature. Unfortunately temperature records are not available for Ain Kahla. In 1968 copulations commenced approximately two weeks after the onset of the autumn rains. Since there was more rain during September 1969 and the copulation season started one and a half months earlier this suggests that rainfall might also be important. Rainfall, however, was often accompanied by lower temperatures and so it remains difficult to determine their relative importance.

Birth Season. During the preliminary study babies were seen. From the start of the population study (9.9.68) until the next April no young babies were seen, indicating that births for 1968 ceased before early September. On 25.4.69 I received a reliable report of a young baby but did not see one myself until 13.5.69. A baby of similar age was subsequently seen in another group. A second baby was born in group 6 on approximately 23.6.69 and no further births were observed in the group before the end of the study. While the sample is small, (intense observations on group 6 prevented the recording of births in other groups) the evidence indicates a birth season from late April through June and probably later, but with no known births after early September. If gestation in macaques lasts 146 - 186 days (Napier and Napier 1967) then the births fall within the expected period. The birth season also corresponds to that found by the MacRoberts' on Gibraltar. Cabrera (1932) observed births in Morocco in May and suggested (from a comparison of two areas) that births occurred earlier at lower altitude.

* See also Michael, Wilson and Plant (1973).
Birth interval. The interval between births could not be determined directly but an examination of group 6 females and their offspring suggests that females did not give birth every year. The behavioural and spatial distribution data that supports the following comments on associations is given in subsequent chapters.

At the start of the 1969 mating season (Sept./Oct. 1969):

(1) Two adult females had babies born during the previous May and June. These were still being suckled and the females were anoestrus and without sexual swellings. One of them (AF 2) associated closely with a juvenile (JF3) estimated to have been born in 1967 and therefore two years older than BF 1. AF 4 was apparently primiparous.

(2) AF 1 and AF 3 were suckling infants (born in 1968) when they started to copulate. AF 3 associated with JF2, estimated to have been born in 1966. If this was her juvenile and she gave birth in 1970 then her three offspring would each be separated by two years.

(3) AF 5 and AF 6 had no unweaned offspring. AF 6's injury (section 3.3.3) may have affected her reproductive ability. She did not associate closely with any animal younger than a subadult female. AF 5 associated occasionally with JM 3 estimated to have been born in 1967.

The evidence for AF 1, AF 2 and AF 3 suggests that females gave birth every other year. This estimate might be compromised by the loss of babies in alternate years but one would then have to assume that after losing a foetus or baby AF 1 and AF 3 continued to suckle their infants born the previous year. Since in macaques juvenile females tend to associate more closely with their mothers than juvenile males, a female that gave birth to males and females in alternate years might give the impression of having had (female) offspring every two years. In group 6 there was only one male young enough to confound the above relationships and since he tended to associate with AF 5 this possibility can be excluded.

Tanaka et al (1970) found with M. fuscata that only 8.6% of females that did not lose infants within 185 days of birth gave
birth the following year. 72% of the one year birth intervals were for females who had lost an infant and 95% of those who had lost infants gave birth the following year. Most females gave birth every other year unless they lost an infant and since M. sylvanus has copulation and birth seasons of similar length, births in alternate years can be expected.

If, as in many non-primate species (Young, 1961), lactation has an inhibitory effect on follicular development (Zuckerman, 1931), the birth interval in a species with a marked copulation season will depend upon the temporal relationship between the cessation of lactation, the period of male fertility and the period of female fertility and receptivity. Only when lactation ceases early enough to permit correspondence between the others can conception occur. Tanaka et al pointed out that if lactation does inhibit follicular development then lactation in M. fuscata must last longer than the 6-7 months originally supposed. Zuckerman (1931) found in M. nemestrina lactation lasted for 8 months with suckling continuing for nearly a year.

In macaques with definite copulation and birth seasons, a one year birth interval might follow if the previous baby was born early in the season. In these cases lactation might cease early enough for the female to conceive late the following year, so giving a birth interval of somewhat more than a year. MacRoberts and MacRoberts (1966) reported that two females that gave birth in May (one before the 22nd, the other on the 26th) began their first sexual swellings on November 19th and copulated. This suggests that lactation lasted for 6 months. It also suggests that AF2 (above) could have been expected to swell and to be receptive in about November. If conception then occurred, that would have given a birth interval of one year, following a two year interval.

More work on the physiological mechanisms is required before the determinants of birth interval are completely understood. This is essential if we are to understand the dynamics of macaque populations. For instance, if the above reasoning is correct a 'perfect' female (i.e. one which, following parturition, conceived in her first fertile cycle that occurred during the mating season and did not abort or lose babies following birth), could have alternate birth intervals of one and two years. Selection would therefore favour as long a copulation season as possible within the constraint that gestation and birth must occur at suitable times of the year.
The study also indicates that care must be taken in estimating annual birth rate by counting the ratio of adult females: suckling young. The ratio found here, 1 : 0.9 (Section 3.3.3) might be taken to indicate one birth per annum if the birth interval had not been determined. This ratio would also vary with the time of the year if females weaned their infants sometime before the birth of the next sibling. Such a ratio is therefore no substitute for data on the number of births per adult female.

3.8. DISCUSSION.

3.8.1. The use of age-sex classifications for macaques.

There is unfortunately considerable variation between observers in the age-sex categories used and the ages of animals included within these. To facilitate comparisons authors should attempt to agree on a convention or at least give the age (or an estimate of this) of the animals. The most similar classification to that used above was given by Bertrand (1969) for M. speciosa. A further difficulty arises from the mixing of strictly sociological or spatial categories with age-sex classes. Imanishi (1963) used the categories 'leader' and 'subleader' males. The former were older and took up a central position in a group feeding at a provisioning site. Do these and Vessey's (1971) 'central' and 'peripheral' males correspond to adult and subadult males? Since no age estimates are given it is difficult to say. It is essential that authors define their categories clearly and extra descriptive tags can then be added as appropriate.

Unweaned monkeys are often divided on the basis of fur colour into two categories; babies or infant 1 and infant or infant 2. 'Infant' is also used to cover both. The age specified for this division varies. e.g. 3 months (M. sylvanus, Burton, 1972), 4 months (M. speciosa, Bertrand, 1969), 5 - 5½ months (this study) and 6 months (M. fascicularis, Shirek-Ellefson, 1967). While my criteria (and also Shirek-Ellefson's) was the completion of the fur change, Burton used the start of this change. Since a dark pelage may signal 'a young animal' to older monkeys (Booth, 1962), this division into two categories based on the change of colouration is, I believe, acceptable. Development is more or less continuous and no
instantaneous change of behaviour is associated with the change of
colour. Infants are gradually treated more like juveniles in agon-
istic encounters. Owing to differences in birth interval, weaning
may occur at different ages both between species and within a popu-
lation. It is reasonable to expect the upper limit of infants to
be defined in terms of an age range. The age given by most authors
falls within that for this project. Sugiyama (1960) used 'infant'
for all monkeys over 1 year but less than 4 years (males) and 3
years (females).

Fully weaned young monkeys are usually classified as juveniles
but the age limits for this category depend upon the limits used for
adjacent categories. For the subadult female category most authors
use the criteria given in section 3.2. Ages quoted vary from 3 to
4 years (Simonds, 1965) to 3.5 to 5 years (and possibly longer) in
this study. *M. mulatta* are sexually mature at 4 years (Koford,
1965) and *M. sylvanus* may conceive as early as 3.5 years (Burton,
1972). The age at first conception will possibly vary between
species with the presence or absence of mating seasons. When this
category is not used these animals are classified as adults (e.g.
Vessey, 1971) or possibly included in both adult and juvenile classes
(e.g. Southwick et al, 1965). The change from subadult to adult
female is clear and not controversial.

There is less agreement on the definition of subadult males and
indeed upon whether this category is required. In *M. mulatta* males
are sexually mature (in terms of spermatogenesis) at 4 years (Koford,
1963) and Vessey and Morrison (1970) classify males of this age as
adults. I believe that the term 'adult male' should be reserved
for sexually mature animals that have achieved full growth and
dentition. This occurs at 6 years in *M. mulatta* (Koford, 1965)
and 7 years in *M. speciosa* (Bertrand, 1969). The period between
attaining sexual maturity and full growth also involves a behaviour-
al transition between the juvenile and adult stages and this is per-
haps the major argument in favour of calling males of this inter-
mediate age subadults. In *M. sylvanus*, for example, these males
started to participate fully in sexual behaviour but their sexual
behaviour was sometimes disturbed by adults; they still on occasions
behaved submissively to some adult females and participated more
actively than adult males in some types of intergroup behaviour. Unlike adult males they did not lead the group or participate in vigilance behaviour. (Details of these and other differences are given in subsequent chapters). In some macaques, males of this age are often spatially peripheral (chapter 13). The term 'subadult' is useful because it shows that in spite of sexual maturity the animals are not yet fully adult. Rowell (personal communication) prefers 'young adult' for these animals but this is less satisfactory since it does not suggest so readily the difference between these and fully adult males. Both terms are preferable, however, to that double-edged term 'peripheral male'.

Burton (1972) classified males of 5+ as adult. These males showed some of the same characteristics as my subadults and her subadult males (3 - 5 years) corresponded in relative frequency of play, size of testes and lack of sexual behaviour to my older juvenile males. The low age at which males achieved 'adult' status on Gibraltar was due to manipulation by the British Army. When a male of 5 years was taken from one group and placed as the oldest male in another, his behaviour was typical of my subadult males. He did not perform the role of 'control animal' and the adult females took over the activities performed by the previously older male (Burton, 1972). Bertrand (1969) and Koyama (1967) classified 4 - 7 year old males as subadults; Simonds (1965) used 3 to <6 years and Shirek-Ellefson (1967) 3 to 5 - 7 years. Prakash (1962) called one to four year olds, subadults.

A further term, immatures, has been used for all animals less than adult (= sexually mature, Vessey, 1971). Koford (1965) excluded from that class monkeys born in the current calendar year.

3.8.2. General discussion.

There are many similarities between the population structure at Ain Kahla and other macaques populations. With the possible exception of M. sinica (Eisenberg et al, 1972) the multimale group seems to be almost universal in natural populations. Group size at Ain Kahla fell within the range known for macaques. Whiten (1972) obtained the following accurate counts for two groups of M. sylvanus in the Moroccan Rif:-
The size of the groups was similar to those at Ain Kahla but since a high ratio of adult males : adult females was found in one Ain Kahla group (table 3.1b) more counts are required before it can be concluded that there were significant differences in composition. The lack of solitary males at Ain Kahla (and also in M. radiata; Simonds, 1965; Sugiyama, 1971) may be attributed to the frequent non-agonistic contact between the males of these species (chapter 13).

Considerable home range overlap has been reported from most populations (e.g. Neville, 1968; Lindburg, 1971 for M. mulatta and Sugiyama, 1971 for M. radiata). An exception may be M. sinica; the home range maps compiled by W. Dittus and published in Hladik and Hladik (1972) indicate that they live in more or less exclusive areas. The Ain Kahla population had a higher degree of overlap than has been reported for other wild populations. This may have been related to population density which was higher than most of the forest populations of M. mulatta studied by Neville (1968) and probably than that studied by Lindburg (1971). Whiten (1972, personal communication) estimated that the range of his two M. sylvanus groups was 2.25 and 2.3 sq. km. This was almost twice the size of group 6's home range and the difference may be related to the more open habitat at Jbel Lakraa. The estimated overlap between the range of these groups was 0.43 sq. km. and it was possible that each group had some area not entered by another.

Now that much of the background information on ecology and behaviour is available for macaques it is time that specific studies of ecology were undertaken. Only in this way can proper comparisons between species be made. An example is provided by the difficulty found when attempting to compare home range size. Different authors use different techniques and time periods to measure this and larger, more reliable samples, are required for each population. Since it took
370 hours to define group 6's range during a stable period it would be difficult to plot accurately the simultaneous ranges of all the groups in a population. Transect techniques or telemetry - checked against sample groups studied in detail - could be used. It is also becoming increasingly important to study population dynamics (Southwick et al, 1970). Vital measurements would include birth and death rates, rate of maturation, change in population size and so on. With natural macaque populations outside India such studies have not yet begun. Adequate conservation programmes can only be based on adequate population statistics.

3.9. SUMMARY.

The criteria used to distinguish age-sex classes and estimates of the age of the animals in these classes are given. Unfortunately there is considerable variation between authors in the categories used and the ages of animals included. To help comparisons age-sex classes should be carefully defined and kept separate from socio/spatial categories.

At Ain Kahla the population structure was similar to other natural macaque populations. The monkeys lived in multimale groups ranging in size from 12 to at least 36 individuals (mean = 24). Larger parties were seen but experience showed that they contained two groups. The ratios between age-sex classes varied between groups. For six groups the overall ratio of adult and subadult males: adult females was close to unity. Details are given of the 25 animals in group 6 - the group subsequently discussed in detail.

Population density was estimated to be 60 - 70 monkeys per square km. The groups had home ranges that overlapped more extensively than has been described for other macaque populations; apparently no group had exclusive use of an area. It took 370 contact hours to accurately establish group 6's home range (1.17 sq. km.) and the ranges for other groups were consequently incompletely known. Water dependent changes in home range may have occurred but this requires substantiating. Although only one death was recorded the ratio of subadult females and juveniles:
infants and babies, suggested a mortality of at least one third between birth and adulthood. People were the only predators known to be successful and are probably the major source of predation throughout Morocco.

Between late January and August the animals moulted; young monkeys moulting later than others. Copulation occurred during autumn and winter; births in the spring and summer. At least two classes of female that were not lactating in the months preceding the copulation season had cycling, incomplete swellings and did not initiate sexual behaviour until they had complete swellings at the start of the copulation season. This suggested a seasonal reduction in female receptivity that was independent of lactation. Females did not give birth every year; a 1:0.9 ratio of females: suckling young was due to infants and babies from different years both nursing. In group 6, births appeared to have occurred every other year but there was some evidence to suggest that a one year birth interval might follow if a female's last baby was born early in the previous birth season.

Since almost all reports of macaque ecology are based on small samples and non standardized techniques this makes comparisons between species difficult and sometimes meaningless.
4. DAILY ROUTINE AND USE OF HABITAT

4.1. INTRODUCTION.

The way in which the group used its home range by moving from one place to another was extremely important. Group movements were a major facet of the daily routine and their nature was probably closely linked with the efficient exploitation of resources. It is against this background of group movement and food searching that I later examine the distribution of social behaviour. Social behaviour played a major role in the initiation of movements and in promoting the dispersal and cohesion of individuals; grooming, resting and other non-agonistic behaviour, not directly concerned with promoting movement and feeding, did intrude but was not predominant until feeding decreased.

One of the problems of working with captive or provisioned animals is that the need for food searching is severely restricted and group movements correspondingly reduced. The modified daily routine makes it difficult to appreciate the partitioning of social behaviour with feeding and movement. It is therefore desirable that studies of wild animals should make this relationship clear as well as analysing the components themselves.

4.2. GROUP MOVEMENTS.

4.2.1. General description of group movements and daily routine.

After sleeping in the cedar trees the monkey became active towards sunrise. Calls were heard and individuals could be seen moving into sunny positions on the ground or in the trees. Once in the sun they autogroomed, scratched, sat (often adopting the sunning position with the upright chest held towards the sun) and small subgroups of allogrooming monkeys formed. Similar behaviour
(with the exception of the sunning position) was seen on cloudy days.

Gradually individuals descended and fed casually, picking up the occasional food item under the trees. When tree-born food items were in season feeding also commenced on these. As more animals descended they either fed under the trees, moved down the forest slopes (if the sleeping site had been on the forest edge), or moved off in a travel-feeding progression. During travel-feeding the predominant activities were moving and feeding. The group was well spaced out, usually with a minimum of one to two metres between individuals and often at least 30 m. The whole group spread out over a ragged elliptical area and moved on a broad front. The distance between the most widely separated animals varied with the circumstances and from group to group; with group 6 it was usually between 100 and 125 m. and occasionally up to 150 m. The presence of two groups together sometimes gave a mistaken impression of group spread (chapter 13). Much faster progressions, involving a narrow file of monkeys, were almost entirely restricted to intergroup encounters (section 5.3.5).

Group cohesion was high and the movement of individuals away from the group was seen only under three special circumstances: (a) During intergroup encounters, when males moved towards another group (section 5.6.2). (b) When consorting animals moved away from the group (fig. 4.1) or perhaps more frequently when they started copulating within the group but were left behind as the others moved on. In the copulation season some adult males (e.g. All, the highest ranking male in group 6) spent periods of up to three hours away from the group. (c) Other movements by adult males, that may have been associated with vigilance behaviour, are discussed in section 7.7.2. A monkey that moved away from the group, or had been left behind allogrooming, glanced towards the group and moved, sometimes running, to catch up with it. Even when consorting monkeys were 200 m. from the group and presumably out of sight, the position of the group was indicated by calls, the sound of stones being turned and branch movements. One rarely heard call, the clear call, was

*Plate 4.1a and b.*
FIG. 4.1.
The movement of consorting animals away from their group. The figure shows the movements of AM1, AF1 (the first consort shown, observed only briefly), AF6 (who followed him and attempted to initiate sexual behaviour) and AF3 (with whom he consorted at length). The dotted lines show the position of the rest of the group.
related to the separation of individuals from the group; it probably signalled the position of the group or a separated individual (section 8.2.9). Grunts may also have influenced group cohesion. These quiet calls (given in brief choruses of antiphonal calling, section 8.2.9) were heard when the group was spread out on the ground feeding. Monkeys feeding at the sides or back of the group often glanced towards other animals, presumably to keep in contact with the rest of the group.

As individuals searched for food items (section 6.3), feeding was interrupted by other activities. A monkey feeding less than about 4 m. from another was likely to be threatened and if it moved within this distance glanced at the other and occasionally teeth-chattered. They tended to keep a distance from each other by walking away from other animals. This was one feature used to rank the individuals; in dyadic interactions the approach-retreat relationship between two monkeys was more or less constant (section 10.2.4). When animals moved away from others (with or without the use of threats) they tended to move in the direction of the group's movement so perpetuating this direction. Following non-agonistic interactions the participants generally moved at least 1 m. apart before feeding recommenced. Larger distances were seen when one interaction swiftly followed another or after agonistic interactions. Smaller distances were seen when babies and infants were involved.

The route taken by a group between the sleeping sites of two consecutive nights is termed the day-journey (Altmann and Altmann, 1970). During the day the rate of movement was not constant and the group tended to slow down or stop around mid-day. This was particularly seen during hot weather and at such times feeding would decrease or stop and social interaction (chiefly non-agonistic) increased. They generally ascended the cedars (or less frequently other trees or remained on the ground) and either sat in a resting posture or participated in allogrooming, maternal care or other interactions involving babies and infants. There was of course considerable flux with monkeys changing partners and moving from one subgroup to another. When tree-born food items were in season they usually fed on these before descending to
continue the day-journey. The day-journey was mainly on the ground with the animals taking to the trees only for sleeping, resting, avoiding predators and, during some seasons, for feeding. When in the trees all age-sex classes (except babies) were capable of jumping from one tree to another. During the day-journey babies and infants were frequently treed, playing while older animals fed.

Feeding was not restricted to travel-feeding periods; frequently the group stayed in one area with the animals moving around in search for items.* This usually happened in the morning, evening and after the mid-day 'rest' period but was also recorded at other times. During some day-journeys the group visited a source of water but the frequency with which this happened varied (section 6.4.1). They often stayed and fed in the vicinity of the wells unless another group approached to drink.

Once in the vicinity of the sleeping trees, feeding continued but other activities (chiefly non-agonistic social interactions) became more frequent as the animals left the ground or trees where they had been feeding and ascended the cedars. The majority of the group were usually in the trees by sunset. Small subgroups formed high in the trees and social interactions continued until it was too dark for observation. No special study was made of their night resting habits. Several trees were used and at least two or three monkeys usually ascended each tree. It is unknown whether they slept alone or in huddles.

4.2.2. Day-journeys.

Day-journeys were recorded by plotting on a map the course of the centre of the group. This was only approximate since it was often difficult to estimate the group's centre of mass (chapter 13). Times were marked on the maps at frequent intervals, usually several times per hour. By becoming familiar with the forest it was possible to record the group's position quite accurately.

*Plate 4-1c
PLATE 4.1(a & b) TRAVEL FEEDING

Note that the monkeys are all facing more or less in the same direction. A juvenile in (b), second on the right, is moving with the hunched walk.
The animals were feeding in one place and not travel feeding. In contrast to (a) and (b) this shows the larger distances frequently seen between feeding individuals.
sites. Fig. 4.2 gives an example of the day-journey on eight consecutive days. The length of day-journeys was measured on the map using a map measurer, each journey being measured three times and the mean measurement converted to km. The mean length of 36 complete day-journeys from the single group study (dates between 14.5.69 and 5.10.69 inclusive) was 1.53 km. (SD, 0.44). Fig. 4.3 shows the frequency with which different lengths of day-journey were recorded. The mean length of 23 complete day-journeys from the population study (dates between 12.9.68 and 23.4.69) was 1.07 km. (SD, 0.64). The difference between the means may reflect three features. (a) The day-journeys may have been shorter when the animals were feeding on cedar leaves. This was most marked on days with heavy snow on the ground; On three consecutive days group 6 moved only 0.30, 0.44 and 0.44 km. These were shorter than any day-journeys recorded during the spring and summer. (b) There were fewer hours of day light available for movement during the winter. (c) The data from the population study was based on less habituated groups with a consequence that the day-journeys may be biased in favour of short journeys when the observer was less likely to lose contact with the group.

Distance between sleeping sites. The straight-line distance between sleeping sites (measured from the middle of the sites) was measured on the day-journey maps. The mean distance between sleeping sites was 0.54 km. (SD = 0.27, single group study) and 0.34 km. (SD = 0.23; population study). Fig. 4.4 shows the frequency with which different distances were recorded.

A comparison between day-journey length and the distance between sleeping sites reveals that on the average group 6's day-journey was three times greater than the distance between its sleeping sites. This emphasizes the meandering nature of day-journeys. For each day there was, however, no correlation between the length of day-journey and the distance between sleeping trees (with a product moment correlation coefficient (Sokal and Rohlf 1969) \( r = 0.009 \), single group study and \(-0.194\), population study).
FIG. 4.2.

Day-journeys on eight consecutive days. The day-journeys taken by group 6 from 28.9.69 to 5.10.69 inclusive.
The length of day-journeys. Based on 38 complete day-journeys from the single group study, May to October.

The distance between sleeping sites. Based on the same data as fig. 4.3.
Rate of movement. A group's rate of movement was not constant throughout the day. It was convenient to analyse the relationship between distance moved and time of day by using the data on time of entry to the hectare quadrats (section 4.3.2) and recording the number of quadrats entered per hour. Ideally one ought to measure the exact distance moved in each hour directly from the day-journey maps. Unfortunately, although I recorded times frequently, these were usually not at regular intervals. A highly significant positive product moment correlation coefficient between the number of entries to quadrats in a day and the length of the day-journey in km. demonstrated that the technique was valid ($r = 0.91; t = 13.6, df = 36, p < 0.001$).

The results for 38 complete day-journeys from the single group study (summer) are shown in fig. 4.5. For most hours the frequency distribution of the number of quadrats entered was positively skewed and hence the median is the best measure of central tendency. The figure shows peaks of movement (in terms of quadrats entered) in the morning and afternoon. Since this was based on complete days only it might be biased against those days on which the group descended early and was missed by the observer (Altmann and Altmann, 1970). The incomplete day-journeys were, however, almost all recorded on days when the observations intentionally started late or ended early and so this can probably be ignored.

The large variation between days means that the complete cessation of movement that often occurred has been obscured. Fig. 4.6 shows that for the hours starting at 1100, 1200 and 1300 there was no movement (in terms of quadrats entered) on approximately 50% of the days and this therefore confirms the pattern shown by fig. 4.5. This midday period of reduced movement was associated with reduced feeding and increased social interaction such as allogrooming (section 4.4.2). It can be termed a rest period. Further examination of the summer day-journeys showed that three main categories could be distinguished. There were, of course, intermediates. (a) Two periods of movement separated by a period of reduced or no movement of up to five hours duration. (b) Three periods of movement separated by shorter periods of reduced or no movement. (c) More or less steady movement throughout the day. During the late autumn and winter the last category became

* The data for each variable approximately followed a normal distribution.
FIG. 4.5. (top)
The distance moved per hour (in terms of the median number of quadrats entered). Vertical bars give the range. Based on the same data as fig. 4.3.

FIG. 4.6. (bottom)
The frequency with which no movement (in terms of quadrats entered) occurred during each hour. Based on the same data as fig. 4.3.
more frequent and if periods of reduced movement occurred these were often shorter than in the summer. MacRoberts (1970) saw a similar change on Gibraltar. The reasons for this seasonal difference are discussed in section 4.5.

A cumulative of the mean number of quadrats entered per hour showed that on average 50% of the day-journey (i.e. 50% of the mean number of quadrats entered) was accomplished by between 1100 and 1200 hrs. This cumulative is subject to the same variation as the means themselves. (The number of quadrats entered per day followed a normal distribution). An estimation of the overall speed of movement during the day-journeys can be obtained from the length of the day-journeys (mean 1.53 km, SD 0.44) and from the fact that movement was restricted to the 13 hours between 0630 and 1830. Division of the mean by 13 gives an estimate of 0.12 km/hr. with 95% of the whole-day speeds falling between 0.09 and 0.15 km/hr. These will be slight underestimates of the speed between actual descent and ascent since the groups often did not move immediately at 0630 and ceased to move before 1930. For the present purposes the above calculation is sufficiently accurate.

4.2.3. Control of group movements.

While travel-feeding the monkeys usually moved slowly on a broad front and in a common direction. A variety of individuals appeared at the front of the group and it seemed that no one monkey was leading the group in the sense of keeping at the front or initiating and maintaining the direction of travel. Each day-journey was unique, there were no long progression routes that were used repeatedly and with little deviation. There were, however, short preferred routes, such as along valleys, up particular slopes and along the edge of the forest. Such routes were frequently traversed in the same way each time the particular area was used and they were linked in innumerable ways into the day-journeys.

On occasions a monkey would move up to 70 m. away from its group in a swift, decisive manner that was usually not interrupted by feeding. Such movements were often followed by the rest of the group moving in the same direction. An individual showing such
behaviour was said to lead the group since it had initiated a move-
ment or change of direction. These movements were seen under the
following circumstances:

(1) When the group was in the trees at morning or midday an animal
was sometimes seen to descend and move away from the trees without
pausing. This was followed by others descending and moving in
the same direction. The reverse occurred on some evenings.

(2) When the group was feeding on one spot or slowly travel feeding,
one monkey would walk through the group. The others would glance
up at it and follow it with their eyes and then either immediately
move in that direction or gradually move there while feeding. The
leading animal sometimes climbed a tree ahead of the group and sat
looking around. Fig. 4.7 illustrates one such initiation of move-
ment.

(3) When the group was travel-feeding in the forest and came to a
small bled to cross the monkeys generally gathered on one side and
did not cross immediately. Several individuals would sit on the
edge of the forest looking around (section 7.3.3) and then one
would get up, move swiftly down and across. The rest of the
group would follow.

(4) During some intergroup encounters one monkey would move away
from an approaching group and was then followed by the rest of the
group.

The proportion of group movements that were started or had
their direction changed as above is unknown; it was only on rare
occasions that the observer could be certain that no other indi-
vidual had preceded the monkey thought to initiate the movement.
Leading animals either kept ahead or were gradually overtaken.
Many travel-feeding progressions stemmed from a gradual spread of
the monkeys which gathered momentum with apparently no single in-
dividual playing a major role. Some movements commenced after
vigorous agonistic sequences. Swift movements were also seen
FIG. 4.7.

An example of the initiation of group movements. Group 6 had been stationary for over 1½ hours (1600 - 1738½). Movement to the north commenced with AM3's rapid movement and AM2's slightly slower movement. AM1 and the rest of the group (enclosed within the solid lines) moved slowly in the same direction.
towards other groups and these were sometimes followed by a change in the direction of the monkey's own group. They were rather specialized cases of the above behaviour and are not considered further here (see section 5.6.2).

Adult males were responsible for almost all acts of leadership during the population and single group studies. One exception, involving three acts of leadership in one hour by an adult female during an intergroup encounter, is given in section 5.3.3, example 4. In the single group study the frequency with which individuals were seen to lead the group in non-encounter situations was AM 1 (5); AM 2 (6); AM 3 (6); AF 5 (1). Leadership was therefore an attribute of the adult male class of animals and not of any one individual such as the highest ranking male. When one male initiated movement the others could be anywhere else in the group and the highest ranking male often came at the back or side of the group. The group also moved as normal when he was copulating 200 m. away.

These swift movements did not always result in the group moving or changing direction. Some of the poorly understood movements by adult males (section 7.2.2) which might be linked to vigilance behaviour, looked like failed leadership attempts. Some responses to swift movements were only local and were replaced by movement in another direction. Presumably monkeys keep animals likely to lead the group under observation, but how do they decide which, if any, to follow and what makes a male lead on some occasions but not others? Does a male's success depend upon the remaining males concurring? It is possible that animals giving leadership movements were simply predicting the group's route and not actually determining it. This is unlikely.

Evidence is later given (section 4.3.3) to show that during day-journeys ground recently used was avoided. This avoidance might well be one function of leadership. It seemed as if during travel-feeding certain individuals initiated the start of movement and its direction and then on each short preferred route, well known to the monkeys, the group would move under its own inertia until the next change of direction was initiated. Groups differed in the speed with which movements started. Group 10 was found to be unsuitable for the single group study since sitting, feeding in one
place was suddenly followed by rapid movements which were difficult to follow. With group 6 there was no such problem. Such differences may depend on the leading animals.

The order of individuals in progressions. It follows from the above that the order of individuals in progressions varied with the circumstances. When a movement had just started under the circumstances noted above then an adult male was almost always at the head of the group. During slow travel-feeding this was frequently not the case.

4.3. USE OF HABITAT.

4.3.1. Introduction.

The discontinuous nature of the forest meant that three principal zones were available to the monkeys; the forest itself, the forest slopes and bleds and the spurs of high ground running down from the forest. The monkeys used all these and they were probably included in the range of most groups. The forest was the centre of their activities and its proximity permitted the exploitation of the other zones where they were more vulnerable to predators.

There appeared to be no regular pattern by which the zones were used. My impression was that slopes and spurs were exploited when the animals were near them, rather than being included with a particular regularity in the day-journeys. After sleeping near the edge of the forest or small bled they often fed on the slopes before commencing the next day-journey. On other mornings a group that slept in the same place fed in the forest and did not appear on the slopes at all. The same applied to feeding in the evening in the vicinity of the sleeping trees. Some day-journeys were spent more or less entirely on the slopes and spurs; on others they were completely excluded. The use of the slopes and spurs was to some extent limited by the presence of the herdsmen's camps; during the winter, when the bleds were deserted, the monkeys came much lower. By using these areas they were exploiting important sources of food. Most of
the junipers and hawthorns grew in these localities and the slopes were covered with stones that were turned to find food. The flora of the slopes and spurs differed from that of the forest floor (section 2.2.2) and probably added numerous species to their diet. The distribution of tree species was also not uniform (section 2.2.2). In group 6's home range most of the oak trees were found on the south facing parts of its range towards the edge of the forest. The group probably spent longer than usual in this area when there were caterpillars in the trees and when the trees were in fruit.

Some parts of the habitat were used more frequently than others by numerous groups. When visiting the wells the groups used the surrounding forest, and corridors in the forest linking the wells to other parts of the area particularly frequently. The repeated movement of groups over these areas probably resulted in some sleeping sites being used more often than at other times.

4.3.2. Range occupancy distribution.

For the single group study it was possible to analyse quantitatively the frequency with which group 6 was seen in different parts of its home range and the daylight time spent there. By placing an overlay that was marked in hectare quadrats (section 3.4.1) over the day-journeys it was possible to determine the approximate time of entry and exit from each quadrat. Times were interpolated linearly to the nearest five minutes whenever the time required fell between two time points (Altmann and Altmann, 1970). It was necessary to apply a correction to the entry/exit times recorded in the field. The time scored for quadrats used for sleeping in (evening and morning) varied according to the time the observer joined or left the group. These times could not be taken from the time of ascent/descent since these were difficult to determine (section 4.4.1) and also varied with the weather, feeding activities and so on. I therefore took these morning and evening times to a common baseline of sunrise or sunset. This was done only when the animals were known to have slept
within a quadrat. The group therefore 'left' the quadrat at sunset and 'entered' it at sunrise. This corrected form of contact hours is referred to as the quadrat occupancy time.

By using this data, the frequency seen in and time spent in each quadrat was calculated (figs. 4.8 and 4.9). These figures cover the whole of the single group study but fig. 4.9 is based only on the occasions when the group was seen to enter (or have slept in) or leave (or go to sleep in) the quadrat. (For this reason times should not be divided by frequencies to give the mean time spent in each hectare). A Spearman rank correlation coefficient (Siegel, 1956) between time and frequency in quadrats was highly significant (when corrected for ties \( r_s = 0.89 \), \( df = 113 \), \( t = 46.21, p < 0.001 \)) showing that the group stayed longer in quadrats that were entered frequently.

There are two possibly significant sources of bias. First, both figures may be biased in favour of quadrats in which the monkeys were frequently located and against those in which the monkeys were frequently left. Simply omitting these quadrats from the records would not completely remove this bias since the bias would presumably decrease over a series of subsequent (or preceding) quadrats. The problem was kept to a minimum by working in periods of several days during which I kept in contact with group 6 from morning to night. To see whether this bias was important I re-examined the data considering only those days on which the monkeys were followed from sleeping site to sleeping site. For both times and frequencies a Spearman rank correlation coefficient between the complete data (figs. 4.8 and 4.9) and the data for complete days was highly significant (when corrected for ties, \( r_s (\text{times}) = 0.96, df = 113, t = 126.6, p < 0.001; \ r_s (\text{frequency}) = 0.97, df = 113, t = 169.6, p < 0.001 \)). As the rank order of quadrats was not affected this suggests that the bias is not operating.

A second possible bias, considered at length by Altmann and Altmann (1970), is that the records may be biased against those areas occupied at times of the day where few observations were made. In the present case, where the habitat was more uniform than savanna, one would expect this to be less important. The above correlations also suggest that this bias was not present.

A cumulative distribution (fig. 4.10) for frequency seen in quadrats (fig. 4.8) and time spent in quadrats (fig. 4.9) shows that a small number of quadrats accounted for a high proportion of the entries and time. The group spent 90% of its time in only 50% of its home range.
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FIGURE 4.8. The frequency with which group 6 entered each hectare quadrat of its home range. Occasions on which the monkeys were seen in a quadrat, but not actually seen to enter it, are included. The co-ordinates used to identify quadrats are along the top and left-hand side. Quadrats underlined are those accounting for 75% of the entries (see p.67). (From the single group study).
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**FIGURE 4.9.** The time group 6 spent in each hectare quadrad of its home range. Based only on the occasions when the group was seen to enter (or have slept in) or leave (or go to sleep in) the quadrad. Quadrats underlined are those accounting for 75% of the quadrad occupancy time (see p.67). Co-ordinates as fig. 4.8. (From the single group study).
FIG. 4.10.
The cumulative distribution of the frequency seen in quadrats (fig. 4.8) and the time spent in quadrats (fig. 4.9). (Time measure used is 'quadrat occupancy time', p. 66.)
**Frequency seen in quadrats:**

22 quadrats (18.8% of home range*) accounted for 50% of the entries.
42 " (35.9% " " " ) " " 75% " " " .
64 " (54.7% " " " ) " " 90% " " " .

**Time spent in quadrats:**

19 quadrats (16.2% of home range*) accounted for 50% of the time.
38 " (32.5% " " " ) " " 75% " " " .
58 " (49.6% " " " ) " " 90% " " " .

* Based on 115 ha entered + 2 ha surrounded but not entered (section 4.4.2).

The quadrats that accounted for over 75% of the entries and time have been marked on figs. 4.8 and 4.9. The area covered by the quadrats that made up the 75% frequency area is termed the 'core area' (Kaufmann, 1962). The frequency area was chosen in preference to the time area since the latter was more likely to be affected by a single but lengthy visit to a quadrat or by the group frequently sleeping in a quadrat. The concept of core area is a statistical one and the decision to use any point as the boundary between areas used frequently and infrequently is arbitrary (Altmann and Altmann, 1970). The 75% level was chosen because the gradient of the frequency curve in fig. 4.10 starts to fall more rapidly in that region. There was also an association between the location of intergroup encounters and the perimeter of the core area (fig. 5.7).

It is important to consider why the group spent such a high proportion of its time in such a relatively small area. Comparison of fig. 4.8 with fig. 3.3 shows that although the core area bordered the forest most of it lay within the latter. Quadrats on the edge of the forest were not used any more frequently than others. No quadrat by quadrat analysis of the vegetation was attempted but there is no reason to believe that there were any major differences between the food resources of this area and most other parts of the home range. A few quadrats to the west of the core area contained relatively few cedars and more regenerating oaks but these were
exceptional. Temporary water holes were not restricted to the core area. The core area contained 80% of the group's sleeping sites (section 4.3.4) despite there being plenty of suitable trees elsewhere. For groups whose home range contains a well this might partially determine the core area. Any shift in a group's home range that was associated with dry season movements to the wells would presumably also influence its core area.

4.3.3. The relationship between the area used on successive days.

The maps for successive day-journeys from the single group study revealed that the group tended to weave backwards and forwards over its range and other groups showed a similar pattern. Day-journeys often started and finished in the core area, where the majority of sleeping sites were located, and day-journeys of the same or earlier days frequently crossed. Less frequently the group moved over several days from one end of its range to the other before turning and returning to the core area. During an eight day period when group 6 was followed continuously, it used about two thirds of its range (fig. 4.2). On another occasion the group was followed for two five day periods separated by three days. During that time it used all but the extreme west and east of its range. The group did not therefore concentrate its activity in one area and then move on to another. Examination of successive day-journeys showed that while day-journeys often crossed, the group infrequently covered the same ground twice on one day and also tended not to go over the actual ground used on the previous day or days (fig. 4.11).
To examine this further I made the following measurements on complete day journeys:

(1) The number of hectare quadrats entered at least once during a day. Entry was defined from the plots of day-journeys (section 4.2.2). Since these recorded only the approximate centre of the group, other quadrats may have been entered by spatially peripheral animals. This gave an estimate of the proportion of the home range used on the day.
Fig. 4.11.
Two examples of the overlap between consecutive day-journeys. A (1.7.69 to 5.7.69) and B (23.8.69 to 27.8.69) should be read independently. Each row across the figure represents a hectare quadrat; the black dots show which quadrats were entered on each of five consecutive days. For example, in A there was no overlap in the quadrats entered on days 1 - 4 but on day 5 some quadrats entered on days 1, 3 and 4 were re-entered.
(2) The number of quadrats entered at least twice on a day. To be included here the estimated centre of the group (as plotted on the maps) had to leave the quadrat and then later re-enter it. This gave the proportion of the range used on the day that was used at least twice. Again this is an approximate measure since the group could enter the same quadrat twice in a day but actually use different parts of it.

When complete day-journeys were available for successive days, the following were also measured:

(3) The number of quadrats entered on the previous day (and where possible on the previous but one day and so on up to four previous days) that were entered at least once on the current day. When the previous day was being considered then the quadrat the monkeys slept in overnight was excluded.

(4) As (3) but the number re-entered on successive days was cumulated to see what proportion of the quadrats entered on the first day had been re-entered at least once on successive days.

Since a different number of quadrats were re-entered from day to day it was necessary to interpret the results in terms of percentage re-entry of the quadrats used on the first day. The results are given in figs. 4.12 and 4.13. There was considerable variation between days and the frequency distributions for 0, 1 and 2 days after the first day were positively skewed. For this reason standard deviations are not given. Under these circumstances the median is a better indication of central tendency than the mean.

Fig. 4.12 shows that a day-journey covered less than 10% of the current day's area at least twice (also shown by day-ranges from the population study), less than 20% of the area entered on each of the previous three days and less than 30% of the area entered four days previously. Fig. 4.13 shows that the area entered on the first day was gradually re-entered on the following four days; while less than 10% was re-entered the same day, 70% of it had been re-entered after four more days. The group entered a mean of 15.6 hectare
FIGURE 4.12. (Top) Percent of quadrats entered on day zero that were re-entered at least once on each consecutive day. (Solid line = mean; dotted line = median; vertical bars = range; N = number of day's data available for each step. Based on the same data as fig. 4.3).

FIGURE 4.13. (Bottom) The cumulative percent of quadrats entered on day zero that were re-entered at least once on each consecutive day. (Convention as fig. 4.12).
per day quadrats ($n = 38$, standard deviation $= 4.7$). This corresponds to 13% of the total home range area.

The results show clearly how the movements of the monkeys were spread throughout their home range and the adaptive significance of this pattern of ranging is considered in the discussion.

4.3.4. Distribution of sleeping sites.

The monkeys slept in cedar trees that were 15 m. or more high. Typical sleeping sites are shown in plate 2.1. The whole group usually slept in a stand of trees which were in canopy connection with each other. On rare occasions (only once during the single group study) the group slept in two parties about 100 m. apart.

Each group had numerous sleeping sites. Group 6, for instance, during the single group study used 35 sites, 11 of which were known to have been used more than once. The visits to each sleeping site were well spaced and they rarely slept in the same trees on consecutive nights. For instance (combining data from the population and single group studies) on only 4% (3/69) of occasions did a group sleep at the same site on two nights running. On 4% (2/46) of occasions they slept in the same trees as the last but one night. For the last but two nights (and so on) the figures were 8% (3/37); 7% (2/29) and 0% (0/25). The mean distance between sleeping sites on consecutive nights was 0.54 km. (single group study) and 0.34 km. (population study) (see section 4.2.2 and fig. 4.4).

Fig. 4.14 records the location of group 6's sleeping sites during the single group study. 80% (28/35) of these were located within the group's core area and a further four sites were in quadrats that immediately bordered the core area. These 28 sites accounted for 84% (48/57) of the total nights recorded. Group 6's home range contained numerous suitable trees and it is therefore relevant to ask why these particular trees were used. Within the forest no reason was discovered. On the edge of the forest some of the sleeping sites were at the head of the small valleys between the spurs. The monkeys fed in the valleys and then moved into the
FIG. 4.14.
The distribution of group 6's sleeping sites during the single group study.
forest and ascended the trees at their head. These trees may have been more sheltered than the more elevated trees on either side. When the animals were moving on the edge of the forest in the evening, they selected trees 25-50 m. into the forest in preference to those right on the edge. Such trees may also have been more sheltered.

During the single group study other groups slept within group 6's range; groups 12 and 13 were known to sleep in the group's core area on three occasions. Since these groups were not followed this certainly underestimates the frequency with which it occurred. During the single group and population studies there were several instances of different groups sleeping at the same sites on different nights. This was most frequent along the routes to and from well 1. When two groups remained united after an encounter they slept in the same stand of trees. Groups slept within 75-100 m. of each other following other types of encounter.

4.4. DIURNAL DISTRIBUTION OF BEHAVIOUR.

4.4.1. Time of descent and ascent of the sleeping trees.

It was difficult to obtain a meaningful measure of these times since in the forest the animals often descended out of the observer's view. When I could see well enough and was sure that the time of ascent and descent was not being influenced by my presence, I attempted to record (to the nearest five minutes) the time that the first animal reached the ground or the last animal left the ground, as well as the time when the majority of the group were thought to have descended or ascended the trees (fig. 4.15). The results may be biased against early descents and late ascents since these were most likely to be missed by the observer (Altmann and Altmann, 1970). No attempt is made to remove this bias.

The monkeys descended from the trees after sunrise and ascended before or at sunset. In the winter and spring there was more day to day variation in the times and they also tended to descend later and ascend earlier. During these seasons the monkeys spent
FIGURE 4.15. Times (in local time = G.M.T) of ascent, descent, sunrise and sunset. Symbols record when the majority of the group of monkeys being watched was thought to have ascended (■) or descended (▲) from the sleeping trees. A and B are respectively the times of sunset and sunrise at Ain Kahla during the study; plotted from calculations by the Royal Observatory, Edinburgh.
more time in the trees feeding and the times were more susceptible to modification by the weather (section 4.5).

4.4.2. Individual activity records.

To measure activity throughout the day and in different seasons, individual activity records (Crook and Aldrich-Blake, 1968) were taken. When I was sure that the behaviour of the animals was not being influenced by my presence or by that of predators, individual activity records were made every 10 minutes. This gave 11202 animal observations in 1243 records spread throughout the daylight hours (fig. 4.16). A record was made by scanning all of the monkeys visible and recording their activity in one of the five mutually exclusive categories given in fig. 4.17. Suckling and being carried were included with sitting, standing and lying; a monkey moving and feeding simultaneously was scored as feeding. A sixth category recorded activities such as drinking, that did not fit into the other categories. The number of animals treed during a record was noted. Records for both years were lumped together.

For each activity the results are expressed as a percentage of the total activity recorded in each hour (fig. 4.17). A more detailed and independent analysis of the diurnal distribution of social behaviour (including allogrooming) is presented in chapter 14. The records have been grouped together into two periods chosen to represent summer and winter. For each period the results will conceal any variation from day to day and the change in sunrise time (40 minutes maximum difference between July and September and 50 minutes maximum difference during the winter) may have smoothed the histograms.

In the summer there were peaks of feeding in the morning and afternoon and a reduction of feeding at midday compared with an increase in sitting, standing and lying, allogrooming and the proportion of animals treed. The increased number treed in morning and evening represents animals in the sleeping trees. There was a slight reduction in the number of animals moving around midday.
FIGURE 4.16. The number of individual activity records made during each hour of the day. 1243 records from 1968 and 1969 combined.
FIGURE 4.17. Individual activity records for 'summer' and 'winter'. The percentage of visible monkeys which were engaged in the mutually exclusive activities, plotted against time of day. (N = number of animal observations contributing to each histogram. 'Treed' gives the percentage treed, irrespective of activity. Data from 1968 and 1969 combined). continued:
FIGURE 4.17. continued.
but animals moving during social interactions prevented this from being the converse of the frequency sitting, standing and lying. (It should be remembered here that feeding included animals that were simultaneously moving and feeding and this explains why the histograms for the resting postures and moving are not mirror images). The day-journeys from the single group study covered a similar period of the year and there are some obvious correlations. The period of reduced group movement between 1100 and 1400 (figs. 4.5 and 4.6) corresponded to an increase in sitting, standing and lying, and also allogrooming, justifying the term 'rest period'. One would not expect a perfect correlation between group movements and the percentage moving, because the group could be static in an area and yet individuals moving actively within that area, feeding and interacting. The peaks of group movement in day-journeys corresponded to the peaks of feeding thus illustrating travel-feeding.

There are some interesting contrasts between summer and winter. In winter there was no midday peak of sitting, standing, lying and in the number treed. Feeding showed an increase from morning to evening while allogrooming showed a marked decrease throughout the day from an initially high level. These differences were also reflected in the day-journeys. In the winter they descended later and movement was more constant often with no rest period around midday. Some of the reasons for this change in routine are discussed in the next section.

4.5. EXTERNAL FACTORS INFLUENCING THE DAILY ROUTINE.

Weather. Differences between group movements in summer and winter have already been mentioned (section 4.2.2) and these were associated with differences in the diurnal distribution of behaviour (section 4.4.2). One interpretation of these results would be that in the winter with shorter days they were forced to forage throughout the day with a corresponding reduction of sitting, standing and lying around midday. The later sunrise and their staying in the trees to feed on cedar leaves accounted for the higher proportion treed on winter mornings. Compared with the summer, the high level of
allogrooming on winter mornings may simply be a consequence of observing a greater proportion of treed animals. As the day proceeded, feeding may have become more important because of the long nights and allogrooming a lower priority activity. Water dependent changes in group movements and habitat utilization were included in sections 3.4.2 and 6.4.1.

Day to day changes in the daily routine could sometimes be attributed to changes in the weather. In the winter there was more variation between days in the time of descent; they often descended up to three hours later on cold, wet days when the sleeping trees were enveloped in low cloud. They fed on cedar leaves or sat in small huddles with their hands pressed to the body and the soles of the feet held together. On the ground they usually fed taking little notice of rain or low cloud. Sometimes in response to heavier rain, snow or hail they sought shelter under bushes or ascended trees and sat close to the leeward side of the trunk often huddled together with two or three others. This led to them being treed earlier than usual. On cold, damp days the hunched walk was frequently used, males often had their testes retracted and monkeys could be seen shaking their fur to throw off the water. Under these conditions and when it was icy they moved in the trees with caution and animals were seen to slip on the slimy branches. Changes in feeding behaviour induced by the snow are given in section 6.3.6. While moving in deep snow they often moved in a single file with each monkey moving more or less in the footsteps of the first monkey (Deag, 1970). Where possible they avoided treading on the snow by moving from rock to rock often sitting on rocks or logs protruding above the snow and also moving to the clear areas under trees before sitting and interacting with others. In winter the sunning posture was used in the morning and at other times of the day, for instance when the sun came out after a shower. When feeding or resting in the summer they actively avoided sitting in the sun; in the winter they often changed position to keep in the sun. A late descent from the sleeping trees in the winter may have been advantageous in permitting the ground frosts to melt before intensive feeding commenced.
Predators. The sighting of predators was frequently followed by the group moving faster, slower or changing direction. If disturbed by the wells they often waited for the danger to pass, drank quickly and then moved off. Earlier ascent, later descents and probably corresponding increases in allogrooming (section 7.3.1) could also be attributed to predators. The sudden appearance of a person was seen to result in the fragmentation of a herd into its constituent groups and also to the unification of two groups that had been moving independently (section 5.3.7).

Intergroup encounters. Many changes to a group's movements occurred during intergroup encounters (chapter 5). Groups often fed in the 'flush' areas near wells until other groups approached to drink.

4.6. DISCUSSION.

It is reasonable to assume that natural selection has favoured the efficient use of resources and the data given in this chapter suggests how this has been achieved. (It should be remembered throughout this discussion that other groups also used group 6's home range). If the monkeys were dependent upon a very clumped distribution of food items, with few clumps available at the time, then one would expect them to concentrate their activities in small, shifting areas corresponding to the clumps of food. This was not the case in this habitat. Here food items were more evenly distributed throughout the range and many were highly seasonal (chapter 6) and available for relatively short periods. Under these conditions it would be advantageous for the group to regularly travel over most of its range so that a high proportion of the available items may be exploited as they become available. If a group uses a home range for many years then selection will presumably favour feeding techniques that permit long term continuity of the food supply and help to maintain its relatively even distribution. When on the ground they were extremely selective feeders (section 6.3) often choosing only a few items from each
place. This may be less damaging to the ecology of the food supply than systematically clearing out a food species from one area. It might also increase (or at least permit an even) feeding efficiency since on subsequent passes over that ground there would be food to collect and not exhausted areas to walk over or avoid.

It follows from the above that if, in the interest of efficiency and long term continuity of resources, the group arranged its movements so as to travel over most parts of its home range then a corollary of this might be an avoidance of areas recently visited. This was suggested by the results given in section 4.3.3. A spreading of activity over the range would also be aided by the abundance of sleeping sites.

How was this pattern of home range use maintained? Did it come about because the monkeys that controlled the direction of group movements were 'programmed' to avoid areas used on previous days; or was it seen simply because the group moved in a semi-random fashion within the constraint that each day-journey must have some of the other characteristics mentioned previously? I believe that the former is more likely; lack of time has prevented me from making the simulations required to investigate the second possibility.

It is unfortunate that the evidence showing a water dependent shift in home range is incomplete (section 3.4.2) since this may also be critical in the efficient use of the habitat. If, except during the dryest years, the group can exploit the forest well away from the permanent water sources, the carrying capacity of the habitat may be proportionally higher. It would be extremely interesting to know which individuals 'decide' when to go outside the normal home range and visit a well. Information on the position of wells is probably stored in the oldest individuals and movement to the wells may be another function of leadership. At a more philosophical level it is possible to suggest that if group cohesion is important, then cohesion may be most easily maintained by restricting the capacity for leadership to relatively few animals such as the members of one age-sex class.
Group movements were a major facet of the daily routine and the background for other behaviour. The monkeys slept in the cedar trees, choosing a different set of trees almost every night and with less than one third of the sites known to have been used more than once. They descended from the trees after sunrise and ascended before or at sunset but these times were subject to modification by the weather or the availability of food items in the trees. During the summer, the day-journeys (route taken between sleeping sites of consecutive nights) had a mean length of 1.53 km. (SD = 0.44) while the mean distance between sleeping sites was 0.54 km. (SD = 0.27). For individual days, however, there was no correlation between length of day-journey and distance between sleeping sites. During the day-journey the group moved on a broad front in a cohesive fashion and the movement of individuals away from the group was seen only under three special circumstances.

In the summer 50% of the day-journey was on average accomplished between 1100 and 1200 hrs. but the rate of movement was not constant throughout the day. Although there were several patterns of movement interrupted with periods of reduced movement or no movement, the general picture was a peak of movement in the morning and afternoon. These peaks of movement corresponded with feeding (travel-feeding). Monkeys allogrooming, resting and the number treed were more frequent when feeding and group movements were reduced. In the winter the midday period of reduced movement was often excluded or reduced and several differences in the distribution of activities are described.

During travel-feeding certain individuals (usually adult males) initiated movements or changes in direction but between these acts of leadership the group moved (with apparently no particular individual determining the direction of travel) along short preferred routes until the next change of direction was imposed.
The use of habitat by one group (group 6) was examined in detail using a quadrat technique. The group spent 90% of its daylight time in only 50% of its home range and stayed longer in those parts of its home range that it entered frequently. The first 32% of the home range (total area 1.17 sq. km.) which accounted for 75% of the entries to quadrats was termed the core area. This area contained 80% of the groups sleeping sites and its perimeter was associated with the group's performance during intergroup encounters. It did not appear to be associated with any major differences in the distribution of resources. Over a period of several days the group entered most of the home range but only ca. 13% of the range was used each day. Day-journeys were characteristically meandering but there was a definite relationship between the area used on successive days that suggested an avoidance of areas recently used. In general a day-journey covered less than 10% of the current day's area twice, less than 20% of the area entered on each of the three previous days and less than 30% of the area entered four days previously. The group took four subsequent days to re-enter 70% of the area used on the first day. It is argued that with the particular temporal and spatial distribution of food items seen in the habitat this form of movement will be an efficient method of exploiting the area and promoting long-term availability of food items. Leading animals may be responsible for this pattern of habitat use.
5. INTERGROUP ENCOUNTERS

5.1 INTRODUCTION.

Although there are numerous reports of intergroup encounters in macaques, there is almost no information from natural forest living populations. The present chapter is an attempt to provide such information and to show that the dynamics of individual involvement in intergroup encounters is an aspect of primate biology deserving close attention. During the early weeks of this project apparent fluctuations in party size made it difficult to understand the grouping tendencies of the population. It was later shown, however, that the fluctuations in party size were due to groups moving in close proximity or uniting (chapter 3).

An intergroup encounter was scored when the behaviour of animals in one group was modified as the result of the behaviour of animals in another. Apart from the first type of encounter to be described, where the changes in behaviour were subtle and usually the result of auditory and not visual contact between groups, intergroup encounters were accompanied by a reduction of the distance between groups. The actual distance between groups varied with the circumstances. With the exception of type A encounters (described below) the definition of encounter used here corresponds closely to the "group interactions" defined by Vessey (1968) and "intergroup relationships" or "intergroup social behaviour" defined by Southwick (1962).

Within this population several different types of encounter were seen. It appeared that the outcome of an encounter depended upon the identity of the groups involved and possibly upon the context of the encounter. During the population study it proved difficult to predict what would happen when two groups met. The single group

* A slightly shortened version of this chapter has been published (Deag, 1973).
study showed, however, that after a sufficient number of encounters it was possible to predict more accurately how the group studied in detail would behave.

5.2 METHODS.

Results from both population and single group studies are presented here. The former was valuable in revealing one encounter type that might have been overlooked if only the single group study had been made. As encounters occurred, I usually stopped other forms of data collection in order to record details of the encounter. The positions of groups and parties were marked on day range maps and times recorded. Encounter details were recorded either by notes or on a tape recorder. Large scale diagrams were drawn in the field to record the movements of individuals as these occurred. These diagrams formed the basis of the figures used in this paper. Where examples of encounters have been given, the field protocols have been edited to avoid repetition and to illustrate most clearly the point under discussion. In the study area groups were unequally habituated to the observer and, so as not to influence the course of an encounter, the observer had to position himself with caution. It was impossible to record full details for all encounters. In some cases observations commenced after the start of the encounter; alternatively the animals were disturbed in some way or obscured by vegetation. Comparisons are therefore limited to encounters for which the relevant details were available, the incompletely observed encounters being excluded. The start and finish time of encounters were recorded and their duration measured to the nearest five minutes (table 5.1). Since the sample size for each encounter type is small, the variation in duration within each type cannot be meaningfully determined. Encounters involving one or more parties (either with or without known groups) are included as intergroup encounters only when they were known to be moving independently previous to the encounter.
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Mean duration of all encounters measured = 86 minutes (N = 30) *

* Excludes any type A or G encounters; ** see text.

Data from population and single group studies.
5.3 TYPES OF INTERGROUP ENCOUNTER.

The encounters observed between groups were varied, but could be arranged on a scale of increasing tendency for the groups to remain in each other's proximity. The encounter types represent points on a continuum of possibilities. The classification must be taken as flexible. It is based on a variety of features that include: the distance between groups, their behaviour at meeting and while together, the duration of the encounter and their movements subsequent to the initial meeting.

5.3.1 Type A encounters. Noticing the presence of other groups.

As a group moved through the forest various noises and calls were made. The response of animals in other groups to these sounds represented the simplest form of encounter. Such simple encounters were of considerable importance for they provided a group with information on the position of other groups. Noises produced by the animals included the knocking of stones, as these were turned in search for food, and the sound of moving branches. Often upon hearing such a sound individuals stopped what they were doing and, after briefly looking towards the source of the sound, resumed their previous activity. Loud calling, for instance during intragroup fighting and calling at predators, lead to the same response. Groups were usually not in visual contact. They responded to calls given almost 1 km. away. No calls appeared to have the primary function of influencing intergroup spacing. More complex encounters commenced with individual groups noticing each other's presence, from sounds produced within each group. There was no noticeable change in the spatial arrangement of individuals following this behaviour, unless this was a prelude to another type of encounter.

5.3.2 Type B encounters. Groups in close proximity with little or no interaction.

This type of encounter can be considered as an extension of type A. It involved a closer proximity of groups (e.g. 40-120m) and a
greater response by each group to the other’s presence. They had a mean duration of 15 minutes (range = 50, N = 7). Groups were usually in visual contact. There was little if any change in the spatial distribution of individuals within the groups, a feature which contrasts markedly with subsequent encounter types. On noticing the presence of the other group, individuals would glance towards it briefly, soon resuming their previous activity. Tree-shaking occurred in some encounters. It was not always possible to observe, under forest conditions, the movements of groups both previous and subsequent to tree-shaking displays. There was therefore a possibility that some type B encounters involving tree-shaking might in reality be type C encounters. Tree-shaking is discussed in more detail later (section 5.6.1.).

Example 1. 22.12.68. Two parties.
As one party crossed a forest track moving north, the second party moved down from the north, sat by the track and crossed to the south. The parties were within 40 m. of each other. No interaction was seen or heard.

Example 2. 4.10.69. Group 6 and a party.
At 1127 AM 1 gave a tree shake. At 1128 AM 2 gave a tree shake and the observer detected a party ca 100 m. from group 6. There was intragroup agonistic behaviour and calling in the party, and group 6 monkeys looked towards this. There was no subsequent interaction.

5.3.3. Type C encounters. Approach - retreat encounters not followed by co-ordinated group movements.

During these encounters one group retreated upon the other’s approach. In contrast to some subsequent encounter types this was not followed by prolonged contact between moving groups. They had a mean duration of 50 minutes (range = 100, N = 10). In this and several other types of encounters adult, subadult and older juvenile males, played a major part in intergroup behaviour. One very characteristic type of behaviour, called here 'intergroup monitoring behaviour', was observed only during intergroup encounters and then principally by these categories of animal. Intergroup monitoring involved a decisive move towards another group, followed by sitting
(principally without feeding or other activity) and looking towards the encountered group in an alert fashion. The dynamics of this behaviour were studied in detail in group 6 and are described later (section 5.6.2). The retreat of one group followed either monitoring behaviour (by individuals from one or both groups) or a more rapid movement towards the other group by either part or the whole of the displacing group. In both cases adult and subadult males were usually the leading animals of the approaching group.

These encounters were observed both near and away from the wells. In both cases one group either displaced the other actively, with agonistic interaction between individuals from different groups, or one group simply moved away as the other approached. Usually the group which retreated from a well was the one that had already drunk. Away from the wells it was difficult to understand the reasons for approach-retreat encounters. In two cases during the course of an encounter the role of displacing and displaced groups was reversed. The encounters varied in the extent to which the approach of one group was directed towards the other.

Example 3. 19.9.68. Group 2 and a party.

The observer had been following group 2. At 1350 members of a party were seen drinking at a well and at that time group 2 gradually advanced feeding towards them. The leading animals of group 2 were two adult males and several infants. The adult males moved forwards approximately five paces at a time, sat and moved again. The party at the well suddenly ran off into the trees behind the well. One adult male returned to drink. At that moment, one of the movements forward by the group 2 males suddenly turned into a run and they chased the party through the trees behind the well. At 1405 the first animal from group 2 drank and a tree-shake was heard from the party. At 1424 another loud tree-shake was given by the party but group 2 monkeys made no move. Under the trees there was an occasional chase but it is unknown whether this involved only the party or both groups. By 1507 group 2 were moving away from the well and at 1520 there were only 9 monkeys left. At 1530, 11 of the party returned lead by two adult males and several juveniles and infants. The remaining animals of group 2 withdrew but there was no further intergroup agonistic behaviour.

Example 4. 2.1.69. Group 8 and a party. Fig. 5.1.

At 0849 when some group 8 monkeys were in their sleeping trees and others feeding nearby, a party was heard approximately 65 m. away. Several of group 8 looked in that direction. Those in the trees descended and joined those feeding. An adult female moved towards
FIGURE 5.1.
Type C encounter. Group 8 avoided a party (Example 4).
Convention for this and subsequent figures. AM ♦, O, SM □, □, JM ▲, ▲, J(unsexed) ▲, ▲, AP □, □, I ▼; unspecified X.

.............. edge of forest or clearing.
(______) lines enclosing majority of group.
→→→→→→ routes taken by individuals or groups.
←←←←←← routes taken by groups before and after encounters.
Numbers, (e.g. 1500) refer to times.
the east and away from the party. Group 8 followed her. The monkeys on the edge of the party appeared, fed and then at 0920 moved west into the forest. At 0923 the same female moved back towards the original position and again group 8 followed her. While the rest of group 8 fed, she moved further west and sat looking in the direction of the party. She climbed a tree and continued looking, again without feeding. At 0950 she descended, moved to the east; as at 0849, and group 8 followed behind her.

Example 5. 19.4.69. Group 11 and a party. Fig. 5.2.

At 1440 the party was heard moving ca 250 m. from group 11. It was on a route which would take it ca 70 m. east of group 11. At 1515 the party had arrived in that position. Members of the party looked towards group 11 after intragroup calling in the latter. At that time a subadult male of group 11 performed a vigorous tree-shaking display. The subadult male and an adult male in the same tree sat looking towards the party. At 1524 they both descended and walked towards the party. At the same time a subadult male of the party ascended a tree and shook it vigorously. Some of group 11 looked in that direction. Following the shake he sat, looked towards group 11 and then descended. While the subadult male of group 11 sat watching the party the adult male sat, watched, advanced and sat. The subadult male fed but the adult male did so only occasionally. The party gradually moved away to the north-east. At 1529 the adult male (group 11) moved down to the tree which the subadult male of the party had shaken, and at 1535 and 1536 shook the tree. Following each shake he sat and looked towards the party. At 1537 the adult male returned to group 11 which had advanced eastwards. The party had moved completely out of sight.

Other cases involved a more complex series of movements. The following example illustrates a case where a group which was first displaced, followed this by displacing the group which displaced it. The example also illustrates how, in some circumstances, a whole group moved directly towards another and settled down in its vicinity. In subsequent encounter types this was often the start of a prolonged contact between groups.

Example 6. 25.2.69. Party and Group 4. Fig. 5.3.

At 1116 an adult male of the party performed a tree-shake. Performed on a living tree this made little noise. He then sat, without feeding, looking towards the north and occasionally autogroomed. At ca 1125 he descended and joined the rest of the party. From 1135 until 1207 this was stationary and feeding. At the latter time group 4 was seen moving swiftly towards the party from the north. Two adult males and two subadult males were at the front of group 4, followed closely by other age-sex classes. Their movement was
FIGURE 5.2.
Type C encounter. Males from group 11 approached a party which avoided them (Example 5). Conventions as for fig. 5.1.

FIGURE 5.3.
Type C encounter. Retreat of a party was followed by retreat of group 4 (Example 6). Conventions as for fig. 5.1.
completely orientated towards the party and the speed was such that some of the last animals were running to keep up with the group. The party took little notice of group 4's approach and most animals continued feeding and facing south. When group 4 got to within 20 m. of the party the advancing monkeys sat and immediately started to feed. At the same time monkeys from the party got up and moved decisively to the south. This was followed by a gradual advance of group 4. The movement picked up momentum and the party moved as a tightly packed unit. There was no feeding. During the initial stages of this movement infants and juveniles from the two groups were involved in chasing but no agonistic calls were given. A single adult male was at the front of the party; the other adult and subadult males were spread out throughout the party. In group 4 two subadult males were in the lead but two adult males later moved so that they were closest to the party.

At 1214 the movement stopped and the groups were positioned as shown in Figure 5. The groups started to feed. While two adult males of group 4 were closest to the party the latter's adult and subadult males were spread out throughout the party. At 1218, following a movement of females, juveniles and infants towards group 4, the adult males of the party moved through and sat closest to group 4. There followed a gradual retreat to the west by group 4. At 1228 males from the party chased members of group 4. After a further chase by the party at 1229, during which agonistic calls were given, group 4 moved away from the party. The final details of separation were obscured by the vegetation.

5.3.4. Type D encounters. Approach followed by sitting together which was not followed by co-ordinated movements.

In this type of encounter either one group moved towards another, or they approached more or less simultaneously. In some cases the whole groups sat, rested and fed in close proximity. In other cases (as in Example 7) the approximation of groups was restricted to the males, the rest of the groups remaining spatially distinct and removed from the encounter zone. They had a mean duration of 57 minutes (range = 120, N = 5). In contrast to the following types of encounter, the groups separated and were not seen to move in a co-ordinated fashion. The separation of groups was casual and did not involve displacement of one group by another. A variation of this encounter type was seen at the wells. There, one group sometimes approached a drinking group and before moving in to drink, waited until the latter had moved. Water was the only localized commodity in the forest and this waiting behaviour was not seen elsewhere. The following example illustrates further the inter-group monitoring behaviour.
Example 7. 4.9.69. Group 6 and a party. Fig. 5.4.

At 1619 the observer became aware of a party 40 - 50 m. to the east of group 6. Eight group 6 monkeys sat looking towards the party. This was done in absolute silence. At 1626 some of the males of the two groups started to advance towards each other (fig.5.) and sat between the groups (fig.5.4). At this time a subadult male from the party gave a tree shake but this produced little sound. From then until 1648 there was further movement of group 6 males. These movements, plotted on fig. 5.4 were restricted to the two subadult males and the oldest juvenile male. The two visible adult males of group 6 remained with the major part of that group. The major parts of both groups actively fed and only a total of three subadult males, one adult male and a juvenile male were engaged in intergroup activities. At 1636 a subadult male and juvenile male of group 6 moved closer towards the subadult male of the party. This moved back a little. A further movement left the two subadult males sitting facing each other and 1 m. apart. At 1648 the party subadult male moved back slightly and an adult male from the party rushed in threatening the group 6 subadult males. An adult male of group 6, having moved into the area without the observer's knowledge, chased one of these. The other subadult male moved back towards group 6. Both the first subadult male and the adult male returned and sat again in front of the adult male from the party. At 1652 group 6 males withdrew as did the party adult male. By 1655 the groups were moving independently.

5.3.5. Type E encounters. Approach, with or without sitting together, followed by co-ordinated fast progressions.

In this type of encounter one group approached another, or the two approached simultaneously. In some cases the two groups sat together as in type D encounters or, as in type C encounters, one group withdrew on the other's approach. In either case this preliminary phase of the encounter was followed by one group walking quickly in front of the other group. Such progressions were swift, the groups moving in a narrow (not necessarily single) file with little feeding. These progressions were therefore very different from normal travel feeding progressions and were more like the swift progressions seen when a group crossed an open area of 'bled' between two areas of forest. Such fast progressions were almost never confirmed under other circumstances. For two complete progressions the speed of movement from the start of the progression until the groups were moving independently was 0.72 and 0.88 km/hr. The distances covered were 0.33 and 0.51 km.
Type D encounter. Males from group 6 and a party approached, sat looking at each other and interacted (Example 7). On the lower figure numbers refer to minutes of 1600 hours. Conventions as for fig. 5.1.
respectively. The speed for one incompletely observed progression of 0.30 km. (total length unknown) was 0.69 km/hr. The mean speed for the two complete progressions, 0.80 km/hr. is eight times greater than the mean speed of the linked progressions seen in type F encounters. Type E encounters had a mean duration of 112 minutes (range = 5, N = 2).

Example 8. 3.6.69. Groups 6 and 13. Fig. 5.5.

At 1126 group 13 was heard calling 180 m. from group 6 and monkeys from the latter group looked towards group 13. Group 13 gradually advanced towards group 6 which had been stationary in its present position for one hour. A group 6 subadult male was on the edge of its group. It stopped feeding at 1209 and sat looking at group 13 for one minute before resuming feeding. An adult and subadult male were the leading monkeys in group 13. At 1211 and 1213 they advanced further towards group 6 having both previously paused and looked towards group 6 without feeding. In response to their movement group 6 animals made no move. The remainder of group 13 moved close behind the adult and subadult male. Monkeys in both groups glanced towards each other. By 1217 group 6 monkeys had started to move east with group 13 monkeys following close behind. By 1225 all monkeys were in a progression moving east and away from the encounter site. By observing various parts of the progression line it was seen that group 6 continued to advance in front of group 13. By 1320 the groups were moving independently. They appeared to have separated by moving at different speeds rather than by changing direction. (In the above example it appeared that the groups kept separate throughout the progression. On another occasion close continuity was noted between the last monkeys of the first group and the leading monkeys of the second group. Two subadult males from one group and one from the other moved in close proximity. Group 6 moved in front of group 13 on each of the three type E encounters between the two groups).

5.3.6. Type F encounters. Approach, with or without sitting together, followed by co-ordinated linked progressions.

This type of encounter proceeded in its preliminary phases like type D encounters. The co-ordinated movements shown by the groups were however very different to that shown by type E encounters. Here groups moved in a linked manner, more or less side by side in contrast to moving one behind the other. Each group moved on a broad front. The speeds of four linked progressions, timed from the start of the progression until the groups were moving independently,
FIGURE 5.5.
Type E encounter. An approach by group 13 was followed by group 6 retreating. Group 13 moved behind it for over 0.5 km (Example 8). Convention: ●, O, positions of groups at times shown; ○, positions of sleeping trees.
were 0.07, 0.22, 0.07 and 0.05 km/hr. The distances covered were 0.34, 1.11, 0.49 and 0.27 km. The mean speed of 0.10 km/hr. is much slower than that characteristic of type E encounters. There is no difference between the speed of linked progressions and normal travel feeding movements through the home range. Both are slow and casual in contrast to the rapid, little feeding movement typical of fast progressions. Type F encounters had a mean duration of 340 minutes (range = 140, N = 4).

Throughout a linked progression the groups were not continually interacting. They drifted together and apart for a variable number of times. The groups appeared to be drawn together by the monitoring movements of the males and the intergroup behaviour was chiefly limited to monitoring and agonistic behaviours. Groups drifted apart apparently by a reduction of monitoring behaviour as the males moved back to catch up with their own groups. On occasions the groups were in close proximity during the period of reduced movement around midday and monitoring was reduced during resting and grooming. In some cases linked progressions were resumed as travel feeding recommenced. Separation finally occurred by the groups moving in different directions or speeds. In the early phases of such encounters each time the groups came together intergroup monitoring usually occurred. In some encounters (not for instance in Example 9) monitoring was noticeably absent when the groups came together during the later stages.

**Example 9. 23.6.69. Group 6 and 13. Fig. 5.6.**

Group 6 was followed from its sleeping trees and it moved independently until 1020 when group 13 was heard nearby. Group 13 approached group 6 and the two groups moved in a more or less coordinated manner until 1730. The groups first interacted at 1044 but the details were obscured by the vegetation. This was followed by group 13 moving behind group 6 and at 1107 the groups interacted again, with the two subadult and one adult males from group 6 performing monitoring movements. By 1130 the groups were separate and although they stayed in the vicinity while grooming and resting they did not meet again until 1512. At that time group 13 approached group 6 and an adult male and subadult male of the former group performed monitoring movements. The groups moved approximately side by side and at 1525 there was some chasing, following monitoring behaviour. This was possibly intergroup antagonism. It was followed by further monitoring by both groups. Males from both groups withdrew and the groups continued independently until 1700 when group 13 again moved close to group 6. Group 6 males advanced towards group 13 in monitoring movements and group 13 withdrew slightly. Monitoring by group 6
FIGURE 5.6.
Type F encounter. Group 6 was approached by group 13 and the two groups moved side by side for over 7 hours (Example 9). * indicates the points where the groups came close together. Other conventions as for fig. 5.5.
subadult males continued until 1730 when they moved back to the main part of their group. The two groups continued to move in the same vicinity but with no further close interaction. The sleeping trees of the two groups were 100 m. apart. The following morning group 6 moved away from the sleeping trees independently of group 13.

5.3.7. Type G encounters. The unification of groups.

Part of the operational definition of 'group' used in this project was that the individuals comprising a group moved as a co-ordinated unit for several days (chapter 3). This definition of a group might, however, be compromised by the finding that two such groups could unite to form a larger unit or herd which moved as an apparently integrated unit for several days. Long term observations would be necessary to determine the proportion of time spent by the groups in the independent and herd states. As the group chosen for detailed study was not observed to unite with any other group such data was not obtained. While the details of this process (in particular the behaviour of known individuals while in a herd) remain to be elucidated, sufficient observations were obtained to describe its occurrence.

Example 10. Group 3 and a party.

When group 3 was located at 1005 on 24.1.69 it was part of a larger unit the exact nature of which could not be determined. Between 1230 and 1300, following a fast progression, during which group 3 maintained a rear position, the groups involved separated. This movement was not unlike the co-ordinated fast progressions seen in type E encounters. From 24.1.69 to 5.2.69 group 3 was followed by the observer on six days. With the exception of an adult male which may have temporarily left the group its size (ca 26 individuals) was, as far as could be determined, constant. On 6.2.69 group 3 met and united with a party but it is unknown whether this was the same party involved on the 24.1.69. Group 3 moved towards the party and until the groups were ca 20 m. apart there was no noticeable change in the spatial distribution of individuals. After this, however, two adult males from group 3 made the first direct approach to the other group and the two united following some intergroup chasing. The groups slept in the same stand of trees. On the second day the groups kept together and moved as one. The adult males from each group appeared to keep closer to the males of their own group, but the adult females appeared to maintain no particular positions. The next morning there were several tree shakes and the groups descended and moved off with considerable chasing. This may have been intergroup antagonism. The groups moved in a fast co-ordinated type progression until lost at 1040.
Groups 4 and 9.

From 0930 to 1245 on 20.3.69 group 4 was observed alone. By 1530 this group had united with group 9 and the two groups moved as one integrated unit from that time until the 23.3.69. On that date between 1000 to 1235 (exact time unknown owing to observational conditions), the groups separated and moved independently. Group 9 was followed. While this was in the vicinity of a well group 4 approached the well at 1435 and united with group 9 at 1505. This took place with no intergroup monitoring behaviour. The animals were completely intermingled and moved again as a single unit. They continued to do so until observation ended at 1015 on 25.4.69.

Less definite examples of unification are as follows. On one occasion a party drinking at a well was disturbed by a herdsman. It ran by the shortest route to the forest some 50 m. away and there united with another party which had previously drunk at the well. The arrival of the two parties at the well was separated by one hour. This and the parties' size and cohesion would indicate that they were separate groups. The herd moved and fed as one unit until lost from sight in the forest 10 minutes later.

On another occasion a large herd of monkeys was seen feeding on the slopes of the forest. This included group 10 and a party. Shortly after observation commenced the herd was disturbed by a man and it separated into two groups, one running north and the other south. Before disturbance no evidence for separate groups was seen. Subsequent observation showed that separation had been complete, no strange individuals being identified in group 10. It has been necessary to exclude from this analysis large parties (some of which contained over 70 animals) when these were not seen to join or divide, and incompletely observed encounters between known groups and parties. It is likely that some of these large parties involved type E, F or G encounters.

Not all encounters fitted into this framework. For example on one occasion two groups met 'head on' and passed through each other with some intergroup agonistic behaviour.

The relative frequency of encounter types is shown in table 5.2. Type A encounters are omitted since these were not systematically quantified. For each group they usually occurred several times a day. During the preliminary study a minimum of 11 encounters were recorded. 9 of these were seen during watches at the wells. They included type C (4), D (1) D or C (1); type B ending possibly in type G upon disturbance (1) and two encounters of unknown type. The two encounters away from the wells were also of unknown type.

It is likely that a localized commodity, such as water, affects the relative frequency of encounter types. Unfortunately, a proposed analysis on the influence of well visiting upon the rate and type of encounter was not possible during the single group study.
<table>
<thead>
<tr>
<th>TYPE</th>
<th>POPULATION STUDY</th>
<th>SINGLE GROUP STUDY</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>All Groups and</td>
<td>Group 6 with</td>
</tr>
<tr>
<td></td>
<td>Parties</td>
<td>Group 12 Group 13</td>
</tr>
<tr>
<td>B</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>C</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>D</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>E</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>F</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>G</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Other</td>
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<td>0</td>
</tr>
<tr>
<td>Unknown</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td></td>
</tr>
</tbody>
</table>

Number of Contact Hours
Encounters Per Hour *

* Type A encounters excluded.
During that summer (1969) these animals were able to obtain sufficient water in the forest and no visits to the wells were made. I believe that type C encounters may be relatively more common at the wells than elsewhere.

The data is inadequate to consider the relationship between a group's size and its performance during encounters. In many cases complete counts of group or party size could not be made and encounters between groups of known size were relatively rare. This is unfortunate since in *H. mulatta* performance in approach-retreat encounters is correlated with group size (Vessey, 1968). In the present study, type C encounters included two in which the displacing group was the larger and one in which displacement of a larger group (29 individuals, minimum) by a smaller one (20) was followed by a reversal of this position. Other types of encounter involved groups of different size as follows: type B (15 and 24 individuals), type D (15 and 24; 23 and ca 47), type 'others' (24 and 35 minimum).

No encounters of types E and F were recorded in the population study. Since it appears, (table 5.2) that the type of encounter varied with the groups involved little can be gained from comparing the overall frequency of encounters in the population study. In the single group study encounters can be divided according to the groups involved. With groups 12 and 13 the encounters fell into restricted parts of the scale: With group 12, group 6 had encounters of types B to D, with group 13 types E to F. It should be noted that some of the encounters with parties could have been with these groups. Group 6 had no type G encounters. Within the limits of the sample size it appears that the type of encounter seen when two groups met depended upon their identity. This is supported by the observation from the population study that groups 4 and 9 had a type G encounter twice. The evidence therefore suggests that pairs of groups may be characterised by the extent of their tendency to remain together during an encounter.

The mean duration for all encounters of known duration was 86 minutes (\(N = 30\)). This does not include any type A or G encounters. The significance of the variation within types (table 5.1), and overall overlap in duration between types, is unknown. This might, however, be expected since there is, in reality, a continuum of encounter types. Data from numerous pairs of groups is also included.
5.4. THE FREQUENCY AND DIURNAL DISTRIBUTION OF ENCOUNTERS.

The frequency of encounters was calculated by dividing the number of encounters (excluding type A) by the contact time (table 5.2). There were 0.033 encounters/hr. in the population study and 0.047/hr. in the single group study. The best estimate of encounter rate is that from the single group study. Group 6 was usually followed for several days at a time and this effectively eliminates error due to short periods of observation. The estimate from the population study, based on several groups followed for different lengths of time, may be subject to such errors. In the population study it was also necessary to eliminate from the records some large parties that were probably engaged in type E, F and G encounters. These were only included when they were observed to split or join, or involved a known group. During the preliminary study with J.H. Crook two watches at the wells revealed 3 encounters between 3 parties in 185 minutes and a minimum of 5 encounters between 6 parties in 215 minutes. It is most likely that the encounter rate was higher when visits to the wells were necessary.

Encounters were unevenly distributed during the day (table 5.4, \( p < 0.05, X^2\) one sample test). Relatively few encounters started after 1500 hrs. No attempt has been made to correct for this in the results presented in other tables.

5.5. THE LOCATION OF ENCOUNTERS.

For the purpose of studying home range phenomena, the study area was divided into hectare quadrats and entry to these was used to define a group's home range. 36% of group 6's home range included 50% of its sleeping sites and accounted for 75% of its entries to the quadrats. This area was arbitrarily designated the 'core area'.* Fig. 5.7 records the position of group 6 during encounters. The three type E encounters were movements away from the periphery of the range towards the core area. The five type F encounters involved movements near, and parallel to, the edge of the core area. Of the remaining eleven classifiable encounters, 9 occurred either at or near the edge of the core area. The three type C encounters that involved retreat of group 6

* See p. 67.
FIGURE 5.7.
The location of encounters within group 6's home range (single group study).
<table>
<thead>
<tr>
<th>TIME OF DAY</th>
<th>NUMBER OF OBSERVATION HOURS</th>
<th>NUMBER OF ENCOUNTERS STARTING IN TIME PERIOD</th>
<th>EXPECTED NUMBER OF ENCOUNTERS</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Before 0900</td>
<td>94.6</td>
<td>7</td>
<td>4.3</td>
</tr>
<tr>
<td>2. 0900 - 1059</td>
<td>100.9</td>
<td>4</td>
<td>4.6</td>
</tr>
<tr>
<td>3. 1100 - 1259</td>
<td>112.3</td>
<td>9</td>
<td>5.2</td>
</tr>
<tr>
<td>4. 1300 - 1459</td>
<td>112.0</td>
<td>6</td>
<td>5.1</td>
</tr>
<tr>
<td>5. 1500 - 1659</td>
<td>108.9</td>
<td>3</td>
<td>5.0</td>
</tr>
<tr>
<td>6. 1700 - 1859</td>
<td>101.7</td>
<td>0</td>
<td>4.7</td>
</tr>
<tr>
<td>Total</td>
<td>630.4</td>
<td>29</td>
<td>28.9</td>
</tr>
</tbody>
</table>

When time periods 1 and 2, 5 and 6 are lumped $X^2 = 3.47$, df = 3, $p < 0.05$.

Data from single group study.
were on the edge of the core area; the fourth, involving retreat of the other group, was in a more central position. After almost every encounter the group either kept within the core area or moved towards its centre. Was the core area a territory? To what extent can the different types of encounter be interpreted as defence of the area and did they result in group 6 having preferential access to the area? This is possible but until more information is available (including data on the relative positions of the core area of adjacent groups) I believe that such speculation should be made with caution. At times when well visits were necessary, or when a group's home range included a well, encounters probably occurred more frequently around the wells and in the corridors of forest en route to them.

5.6. BEHAVIOUR DURING ENCOUNTERS.

5.6.1. Tree-shaking.

Tree-shaking occurred during intergroup encounters and also at times when no other monkey groups were known to be near. In the latter situation, another group was sometimes seen near after the tree-shake had occurred. It is not, of course, known how many times another group was close, but obscured from sight by the vegetation. Tree-shakes were seven times more frequent during encounters than during non-encounter periods (table 5.4). The data in this table is restricted to the single group study where the data for non-encounters and encounters is directly comparable. Before and after shaking the animal usually sat looking towards the other group. Sitting and looking around appeared to be less frequent during non-encounter situations.

Tree-shakes were recorded in 46% of encounters (18 out of the 39 for which data was available) and during most encounter types. Owing to the small sample it is not possible to analyse the tendency for tree-shaking to occur with different types of encounter. During encounters the context of tree-shaking was variable. In some cases (particularly during type B encounters) the animal shook without first moving towards the other group. On other occasions it was given after the initial approach towards another group. In
<table>
<thead>
<tr>
<th>AGE-SEX CLASS</th>
<th>Not during encounters</th>
<th>During Encounters</th>
</tr>
</thead>
<tbody>
<tr>
<td>AM</td>
<td>11</td>
<td>6</td>
</tr>
<tr>
<td>SM</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>JM</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>AF</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>SF</td>
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<td>0</td>
</tr>
<tr>
<td>JF</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Unsexed J &lt; 2 yrs</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>I/B</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Unidentified</td>
<td>8</td>
<td>11</td>
</tr>
<tr>
<td>Totals</td>
<td>38</td>
<td>20</td>
</tr>
</tbody>
</table>

Number of:
- contact hours: 585.1 45.3
- shakes/hour: 0.06 0.44

* principally animals heard but not seen to shake.

Data from single group study.
both displaced and displacing groups shakes were recorded both before and after the withdrawal of the displaced group. Examples 3, 4 and 5 (earlier) provide typical examples of tree-shaking during encounters. Since other behaviour occurred during encounters, it is difficult to determine the effect of tree-shaking per se upon another group's subsequent movement. The shaking generally had little effect upon the individuals of the shaker's group. The animals usually ignored the movements and sound, or simply looked towards the tree-shaking monkey. It produced no immediate change in the group's movement or spatial distribution. Tree-shakes from other groups produced the same lack of reaction. This behaviour was never used as part of an intragroup threat sequence.

Table 5.4 records the age-sex class of the group 6 individuals known to tree-shake during the single group study. It is based on the number of tree-shaking bouts. Bouts were considered separate from previous and subsequent bouts if they were separated by other activities, such as sitting and looking around. In non-encounter situations a variety of age-sex classes shook trees. Young juveniles (ca < 3 years) and infants performed those movements as part of play sequences, either alone or with their peers. Such shakes rarely produced an appreciable noise and were accompanied by either running and leaping through the branches or social play. During encounters only adult and subadult males were identified as tree-shakers and this emphasizes again the importance of these age-sex classes during encounters. Table 5.4 is based on visual and auditory information. In some cases the latter led to the tree-shaking animal being seen. There might therefore be a higher probability of including an animal in such a table if its shake produced noise. Combining tree-shaking in encounter and non-encounter situations, the frequency with which individual group 6 males shook was as follows: AM 1 (10), AM 2 (4), AM 3 (2), SM 1 (4), SM 2 (0), JM 1 (1). (Plus one by either AM 1 or 2 and one by an unidentified juvenile male. Based on single group study). In this group there was therefore a positive correlation between the numbers of shaking bouts and rank within age classes. While subadult males shook during encounters, this was relatively infrequent compared with their high level of intergroup monitoring behaviour (section 5.6.2).
Occasionally it seemed that tree-shaking outside encounters was stimulated by the observer's presence. In these cases the shake sometimes followed a movement by the observer and the shaking animal then sat and looked towards him. This was recorded in 7/54 tree-shakes during non-encounter situations (population and single group study data). The frequency with which this occurred appeared to decrease as the group became more habituated to the observer's presence. Compared with the number of occasions on which it did not occur, tree-shaking at the observer was a very rare event.

5.6.2. Intergroup monitoring behaviour.

This term refers to a behaviour seen only during intergroup encounters. Intergroup monitoring behaviour involved a decisive move towards another group (monitoring movements) followed by a prolonged period of sitting in the encounter zone, i.e. the area between the two groups. Such animals sat in a relaxed posture, alert and looking towards the other group (plate 5.1). Monitoring animals only occasionally fed or engaged in other activities. A monkey from one group occasionally moved back in response to movements by an individual from another group. It is important to note, however, that for most of the time these animals did not show any overt threatening behaviour. For instance, during monitoring movements an animal would stride easily and was alert. It did not, however, push its head forward in a threatening posture or lunge towards the animals of the other group. While prolonged staring may be a form of threat, the seated animals did not raise their eyebrows or push their heads out towards the animals from the other groups. Occasionally, monitoring animals subsequently did threaten and chase individuals from other groups. Then the agonistic behaviour patterns seen during intragroup behaviour were used. Monitoring animals were silent. Individuals from each group took up positions facing each other. Movements across the encounter zone by members of one group were followed either by eye or with a corresponding movement in the other group. As explained earlier (5.3.3) monitoring behaviour was sometimes followed by one group retreating.
Monitoring movements showed that the spatial distribution of individuals in one group was directly affected by the other group's presence. In most non-encounter situations there was no evidence to suggest that some individuals were spatially central or peripheral (chapter 13). In encounters where monitoring movements were seen this position was clearly changed; the individuals engaged in monitoring behaviour took up positions in the encounter zone. Individuals nearest to the other group did not simply turn around to face it. This occurred, but they also moved from all parts of the group to take up positions between the two groups. Although the distance between monitoring animals of opposite groups varied considerably, they were usually closer to each other than they were to the majority of their own groups. On occasions they were only one metre apart; a more frequent distance would be 5-10 metres. While these individuals were in the encounter zone, the majority of individuals from both groups were not involved and intragroup activities would proceed as in the non-encounter state. This does not mean that these individuals were not affected by monitoring behaviour. In several cases, particularly type F encounters, the whole direction of group movement was changed. Here the remainder of the group eventually moved up behind the monitoring animals.

81% of group 6's encounters were known to include monitoring behaviour (table 5.5). Since, by definition, it was excluded from type B encounters, the proportion for other encounter types was effectively higher. Intergroup monitoring behaviour was primarily an activity of adult, subadult and juvenile (ca > 3 year) males (table 5.5). The number of encounters in which individual males (J. and older) were known to monitor were compared ($\chi^2$ one-sample test) with the number expected if all males monitored equally. The males differed significantly ($p < 0.001$), owing to subadult males monitoring more frequently than expected, and some other individuals monitoring less often than expected. Juvenile and adult males appeared to monitor in relatively short bouts. No quantitative data on time spent monitoring was however collected. The population study confirmed that this behaviour was characteristic of the population. The proportion of the male age-classes in each group and individual differences in behaviour, may produce a small difference
**TABLE 5.5**  
**GROUP 6 ANIMALS SEEN TO PERFORM INTEGROUP MONITORING BEHAVIOUR**

<table>
<thead>
<tr>
<th>ENCOUNTER TYPE</th>
<th>NUMBER OF ENCOUNTERS KNOWN TO INCLUDE MONITORING</th>
<th>NUMBER OF ENCOUNTERS FOR WHICH DATA IS AVAILABLE</th>
<th>Number of encounters in which individuals were observed to monitor:</th>
</tr>
</thead>
<tbody>
<tr>
<td>B (4)*</td>
<td>0</td>
<td>3</td>
<td>AM1 AM2 AM3 SM1 SN2 JM1 JM2 JM3 Others</td>
</tr>
<tr>
<td>C (4)</td>
<td>3</td>
<td>3</td>
<td>0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>D (3)</td>
<td>3</td>
<td>3</td>
<td>1 0 1 3 1 1 0 0 0</td>
</tr>
<tr>
<td>E (3)</td>
<td>3</td>
<td>3</td>
<td>1 0 0 3 3 2 0 0 0</td>
</tr>
<tr>
<td>F (5)</td>
<td>4</td>
<td>5</td>
<td>0 0 0 2 3 0 0 0 0</td>
</tr>
<tr>
<td>G (0)</td>
<td>-</td>
<td>-</td>
<td>- - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -</td>
</tr>
<tr>
<td>Unknown (11)</td>
<td>4</td>
<td>4</td>
<td>2 0 0 3 4 2 1 0 J and SP</td>
</tr>
<tr>
<td>Totals (30)</td>
<td>17</td>
<td>21</td>
<td>7 2 2 14 15 6 2 0 2</td>
</tr>
</tbody>
</table>

Number expected if all males monitored with equal frequency.  

\[ \chi^2 = 30.33, 7 df, p < 0.001 \]

81% (17/21) of encounters were known to include monitoring.

* Total number of each encounter type. Data from single group study.
between groups. An adult male in group 13 appeared to monitor more
frequently and with greater persistence than any group 6 adult male.
Group 12 adult and subadult males seemed to monitor less than those
of group 6. While females and other juveniles would look towards
another group and occasionally pause and watch it between bouts of
feeding and other activities, they rarely performed the full monitor-
ing behaviour. An interesting exception is provided by Example 4.

To illustrate the details of intergroup monitoring behaviour the
following example is given. Example 6 illustrated the initial move-
ments of males towards another group and gave some details of monitor-
ing behaviour. In the following example it was possible to plot the
positions of most of the group members.

Example 12. 2.9.69. Groups 6 and 13. Fig. 5.8.

This encounter (type F) commenced at approximately 0955 with a
tree shake by a member of group 6. Group 6 was stationary. Group
13 gradually moved south towards group 6 and by 1130, when group 13
was first seen by the observer, the two groups were in close proximity.
Intergroup monitoring was in progress. Fig. 5.8. records diagramti-
cally the positions of 21/25 group 6 individuals.

While the diagram plots the movements of individual males, it is
perhaps more important to note the overall effect of a band of monitor-
ing group 6 males in the encounter zone. Only one female entered this
zone and this was IF 2. She is shown elsewhere to be spatially close
to the group’s males. She did not engage in monitoring behaviour.
The majority of the group, known to include adult and subadult females,
babies, infants and one adult male, were located approximately 40-50 m.
from the encounter zone. These animals stayed there from the beginning
of the encounter until they moved north at 1240. By that time the
intergroup monitoring had more or less ceased and group 13 was slowly
moving away to the north west. The monitoring individuals were AM 1
and AM 2; SM 1 and SM 2; and the oldest juvenile males JM 1 and JM 2.
In group 13 the closest individuals were two adult males. The activi-
ities of the two groups' males were correlated. For instance at
1130 SM 1 sat facing a group 13 adult male. At 1139 SM 2 moved position
and took up a new position at 1142. During this movement the
group 13 adult male followed him with his eyes and then moved to a
new position as shown. At 1152 SM 2 moved again and the group 13
adult male moved around and eventually took up his 1155 position.
These movements were followed by further movements in the same direc-
tion by both groups. At 1223 AM 2 ran at an unidentified group 13
monkey. By that time most of group 13 had moved slightly north-west
and continued to do so. With the exception of AM 1 and AM 2 the
monitoring by group 6 monkeys had ceased by 1220. The two subadult
males and one juvenile male fed, and at 1227, two of these moved back
to the rest of the group (as shown) in response to a call given by a
baby male. The major part of the group moved north-west at 1240.
By then, monitoring had been relaxed and AM 2 moved from his last
FIGURE 5.8.
The movements of individual males during intergroup monitoring behaviour (Example 12). Superscripts (e.g. $^1$) give the rank within age-sex classes. Conventions as for fig. 5.1.
monitoring position at 1238. While group 13 remained near, the behaviour of group 6 was then directed towards intragroup activities with only occasional glances towards group 13. At 1400-1430 group 6 moved after group 13 and the two moved side by side in a co-ordinated, linked progression until separating at 1530. During these subsequent movements monitoring behaviour was reduced in frequency and at times absent.

The possible functions of monitoring behaviour are examined in the discussion.

5.6.3. Agonistic behaviour.

Encounters were analysed according to the presence or absence of overt agonistic behaviour and agonistic contact between monkeys of different groups. Overt agonistic behaviour refers to any aggressive behaviour pattern in a series, between either the tense-mouthed or staring open-mouthed pout faces (both with head pushed towards object) and actual attack. Agonistic contact refers to any attack which lead to physical contact between the fighting animals. For those encounters which were seen clearly, 46% (6/13) of the population study encounters and 50% (10/20) of the single group study encounters involved overt agonistic behaviour. No cases of agonistic contact were recorded. This reflects the low level of agonistic contact seen during intragroup behaviour. It is important to note the low level of wounding in these animals. Only one fresh wound involving broken skin was observed. Owing to the small sample it is not possible to discuss the relationship between encounter type and the occurrence of overt agonistic behaviour. It was recorded in all types of encounter with the exception of types A and B. This exception would be expected by definition.

Agonistic interactions between individuals of different groups usually started with one of the males engaged in monitoring behaviour, threatening or being threatened by another (see plate 5.1). Females, younger juvenile males and infants became involved primarily when chasing brought monkeys from one group towards the major part of another. Table 5.6 lists for group 6 the involvement of age-sex classes in intergroup agonistic behaviour. Only males were aggressors. The proportion of adult : subadult males involved was as expected from their relative proportion in the group. In contrast,
<table>
<thead>
<tr>
<th>NUMBER OF INTERACTIONS</th>
<th>AM</th>
<th>SM</th>
<th>JM</th>
<th>AP</th>
<th>SF</th>
<th>JF</th>
<th>I/B</th>
<th>Unidentified</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aggressors</td>
<td>7</td>
<td>4</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Victims</td>
<td>0</td>
<td>10</td>
<td>4</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>4</td>
<td>5+*</td>
</tr>
</tbody>
</table>

* Unknown number from two interactions.

Data from single group study.
PLATE 5.1(a-d) AGONISTIC BEHAVIOUR DURING AN INTERGROUP ENCOUNTER

Black arrows point to members of group 6 (B), white arrows to members of the other (W). In the encounter zone a WSM (almost adult) sat facing a BSM and a BSM and BJM were grooming (a). Approach of the WSM, followed by a threatening gesture (b) broke up the grooming pair (d). Subsequently, this WSM chased the B group animals until he was himself chased by a BAM (d). The seated posture of the BSM on the left in (c), was typical of intergroup monitoring animals. (Group 6 animals in (a) are, from left to right, SM1, SM2, JM2 and in (d) AM2).
while adult males were never victims, subadult males were victims frequently. This involvement of males (particularly subadult males) is related to their close proximity to other groups during encounters.

In some cases agonistic interactions commenced with an adult male running towards the monkeys at the edge of the other group, without previously performing monitoring behaviour. Threatened monkeys ran back towards their own group. This was followed, in some cases, by adult and subadult males from the victim's group running to the encounter zone. These animals either, threatened or chased the victim, took up monitoring positions, or threatened individuals from the other group. Plate 5.1 gives an example of such an interaction. The squealing of females and young animals appeared to be particularly effective in bringing adult males running to the encounter zone. Once there, they often stayed in the zone only briefly. In contrast subadult males often continued monitoring until the groups finally separated.

5.6.4. Non-agonistic behaviour.

No intergroup non-agonistic behaviour (other than monitoring) was observed in encounter types A to F. Since the single group study included only a short part of the mating season, the absence of intergroup copulation needs to be confirmed. There is probably extensive contact between individuals of different groups during type G encounters but, as so few individuals could be recognized at that stage, only one was confirmed: A subadult female groomed an infant from another group.

5.7. INTERGROUP ENCOUNTERS IN OTHER MACAQUES.

5.7.1. The frequency of encounters.

Intergroup encounters have been observed in most of the studied macaque populations. Two exceptions are the studies of Nolte (1955, M. radiata) and MacRoberts (1970, M. sylvanus, on Gibraltar). Few studies give details of encounter rates. Vessey (1968), working with the La Cuevan rhesus, reported 0.36 encounters/hour. On
Cayo Santiago, Loy (1970) recorded 1.1 displacements/hour. Lindburg (1967 p.99) reported that in India "rarely did a group pass through a day without coming into contact with at least one of the other four groups in the area". One can therefore infer that the encounter rate was lower than those quoted above. In a less densely occupied forest habitat he found that encounters were less frequent *. In the present study the rate was 0.047/hr. These differences reflect differences in population density and patterns of habitat use. The mean duration of 204 encounters on La Cueva was 7 minutes (Vessey, 1968); much shorter than the mean duration of 86 minutes recorded in the present study.

5.7.2. Types of encounter.

Most encounters described for other populations fit into the classification used in this chapter. Type A and B encounters probably occur in most populations but have almost never been reported. Type C encounters have been seen in M. mulatta, M. radiata, M. fascicularis, M. silenus, M. cyclopsis and M. fuscata. On Cayo Santiago Island, La Cueva Island and in the Indian temple habitats (M. mulatta), type C encounters are exaggerated in frequency by high population density and localized sources of food. They are also more violent, involving extensive intergroup fighting (see 5.7.3).

Of the 112 type C encounters observed by Wilson (personal communication) on Cayo Santiago, only 13 were away from the feeding stations. Sugiyama (1968) observed type C encounters between M. silenus groups when they came into contact at food trees.


* See addendum.
hierarchy, revealed by approach-retreat encounters. A group's rank may also be based on the relative rank of the highest ranking males (Koyama, 1970; Koford, 1963; Vessey, 1968). One group may, however, recognize the other's status without seeing the highest ranking male (Koford, 1963).

According to Vandenbergh (1967) a group's rank may depend upon its 'central group of females' since group rank did not change when high ranking males changed groups. Vessey (1968, 1971) speculated that 'peripheral males' may play an important role in determining group rank; when he removed alpha males this had no effect on group rank. Marsden (1968 b, 1971) has shown in enclosed groups that "instability of intergroup dominance can be experimentally induced by the removal or introduction of young, 'peripheral' males". Several of these studies report reversals of the intergroup hierarchy. These may depend upon the locality of the encounter (Southwick, 1962; Furuya, 1965).

Encounters approximating to type D have been reported by several studies (Rahaman and Parthasarathy 1969 a and b; Sugiyama, 1968, Wilson, personal communication). Vandenbergh (1967) found that in 6% of 92 encounters the bands "remained together for one to fifteen minutes duration without antagonism". This occurred between two groups in particular. Working on the same population Vessey (1968) noted that two groups remained close for up to three hours. He also reported encounters, lasting up to 45 minutes, which correspond to the type E encounters described here. On La Cueva, type C encounters developed into type E encounters when the two groups were moving along a common pathway, one group being continually pushed in front of the other. This explanation does not, however, fit for the present study. In the more uniform habitat of the Ain Kahla forest, special pathways were not defined.

It is speculated later that type G and F encounters may be more common among related groups. Evidence for or against this might be found in studies of group division. Unfortunately most of these studies give little detail of the ranging patterns of the groups prior to, during or after division. Southwick et al (1965) found that in M. mulatta the groups became increasingly independent and their relationship with each other increasingly antagonistic. In
M. fuscata studies of group division have concentrated upon the social changes within the dividing group (Furuya 1960, 1966, 1969; Koyama, 1970). According to Furuya (1968) division occurs abruptly. Sugiyama (1960), however, found that the branch troop became gradually more and more independent until separate sleeping sites were used. From that point the groups were fully independent and encounters between them led to no unification, temporary or otherwise. Nothing is known of group division in M. sylvanus and so comparisons should be made with caution. If division occurred in a similar way then type G encounters would represent an early stage in division. My impression, admittedly based on little hard evidence, is that type G encounters represent either the late stages of division or a post division behaviour. Type F encounters have not been described in any other macaque.

5.7.3. Agonistic and non-agonistic behaviour.

One important result of the high population density of the Temple habitat and Cayo Santiago rhesus populations may be that the animals have become, in one respect, habituated to the frequent close proximity of other groups. Sounds from one group do not seem to warn of another group's presence. Apparently, type A encounters carry no meaningful information. Southwick et al (1965) and Southwick (1962) reported rhesus groups surprising each other, since they relied on visual and not auditory cues to detect another group's approach. On Cayo Santiago the banging of hopper lids may indicate that a feeder is occupied; calls apparently do not. The surprising of groups and the blocking of retreat in urban areas may be responsible for the almost extensive daily occurrence of intergroup fights (Southwick, 1962). Southwick (1962) classified rhesus encounters as "usually antagonistic" with "direct overt fighting between groups". Lindburg (1967, p.99) reported that in the Asarori forest, where encounters were "relatively rare", they were "invariably marked by a high degree of antagonism". This was in spite of population density in the forest area being lower than at his other study site. Encounters in the forest population studied by Neville (1966) appear to have been less violent. Probably only
one out of ten encounters involved fighting between groups. In 219 encounters Vessey (1968) saw 3 cases of agonistic contact. Wilson (personal communication) saw 10 cases in 112 type C encounters. Vandenburgh (1967) recorded gestural and vocal threats in 12% of 92 encounters and fights in 22%. Wounds are common in some Cayo Santiago animals (Koford, 1965). In both the present study and Vessey's (1968), ca. 50% of encounters included overt agonistic behaviour. Neither the frequency of agonistic contacts, nor the proportion of encounters involving overt agonistic behaviour, fully reveal the more violent nature of encounters in *M. mulatta* when compared with the study population of *M. sylvanus*. A more sensitive measure is required for adequate comparison. Encounters in *M. radiata* (Rahaman and Parthasarathy, 1969b) and in *M. fascicularis* (Shirek-Ellefson, quoted by Marler, 1968; Furuya, 1965) may also be violent.

Other studies have noted the involvement of adult and subadult males during encounters (Rahaman and Parthasarathy, 1969b; Southwick, 1962; Koford, 1963b; Marsden, 1968a, b; Neville, 1966; Sugiyama, 1960, Wilson, personal communication). Vessey found that 'peripheral males' were most often involved in the overt aggression between groups and this is upheld by the observations of Marsden (1968a). Vessey concluded that involvement correlated with the spatial distribution of individuals within the group. This is supported by Neville's (1966) observations on wild, forest living animals. The present study, however, shows how the presence of another group produced a marked change in the spatial distribution of individuals. Involvement could therefore be explained primarily in terms of movement into the encounter zone rather than the relative positioning of individuals in the non-encounter state. This highlights the active participation of these age-sex classes.

Non-agonistic contact between individuals from different groups has been reported. Wilson (personal communication) observed intergroup copulation and grooming. Nishida (1963) only saw intergroup copulations when the groups were brought together by artificial feeding. Some 'intergroup copulations' involve males actually changing groups (Lindburg, 1967). Vessey (1968) saw intergroup play and copulation.
5.7.4. Tree-shaking and intergroup monitoring.

Tree, branch or timber, shaking during encounters by adult or subadult males has been reported from most studies. Altmann (1962) considered that timber-shaking, in the Cayo Santiago rhesus, indicated an occupied region, but it was not given at any territorial boundary. Marler (1968) classified it as a signal that increased the distance between groups; if this were the case in the study population one would expect tree-shaking to be more frequent during the early encounter types. In the two cases when tree-shaking was recorded during type G encounters, the unified groups appeared to be in the preliminary stages of separation. Southwick (1962) considered tree-shaking to be a form of threat. While this may be so, it is not essential to the interpretation of the behaviour as a signal that increases the distance between groups. *M. fuscata* call while tree-shaking and these calls are related to calls given during agonistic situations. Tree-shaking is given during intergroup encounters, following intragroup fighting and leader males use tree-shaking to indicate the departure of the troop and its direction of movement (Itani, 1963; Yamada, 1966). Rahaman and Parthasarathy (1969 b) considered that branch-shaking had two functions; signaling the presence of one group to another and warning group members of the other group's approach. Branch-shaking outside encounter situations has been recorded by Altmann (1962); Itani (1963) and Simonds (quoted by Marler, 1968). Marler (1968) suggested that this may function as a signal that maintains the distance between groups. In the present study it occurred too infrequently to be ascribed this function. *M. silenus* has a loud whooping call, given by large males, with the apparent function of influencing intergroup spacing. Given during encounters, one group moves away after a short period of calling (Sugiyama, 1968). Adult male *M. fascicularis* call before and during movements and this is thought to keep groups spaced out (Shirek-Ellerson, quoted by Marler, 1968).

Intergroup monitoring behaviour has not been discussed in detail for any other macaque. Simonds (1965 p. 195), however, noted that:
"When the two groups met the subadult and adult males would move towards the other group, and then sit and look at each other with approximately 20 ft. between them. Then the males in one of the groups would begin to drift back in the opposite direction and the groups would separate."

This closely corresponds to the behaviour described in this chapter.

5.8. DISCUSSION.

The encounters described for this population cannot be explained simply in terms of a group dominance hierarchy. Some groups clearly displaced others (type C encounters) and, with a larger sample, it might be possible to show that the approach-retreat relationship of groups was relatively constant. The remaining encounters do not fit into this limited theoretical framework. To call type D encounters 'stalemates', because they result in no displacement, has no explanatory value. A wide variety of factors most likely influence the nature and frequency of encounters. Table 5.7 lists some of these. (See also Bates, 1970). Only long term studies of a population could fully determine the relative importance of these factors. The purpose of the following is therefore to speculate how some of them may have influenced the encounters recorded in this paper.

Ranging characteristics determined which groups could possibly meet. Group 6 met group 12 less often than group 13, most probably because it had greater home range overlap with the latter. The individuals within groups that met frequently may have been more familiar with each other's behaviour and encounters and may therefore have proceeded differently to those between groups which met less often. This may be one reason for the different types of encounter between group 6 and these two groups. At some seasons one might expect a higher encounter rate at wells and it is likely that at such times groups would encounter groups from outside their own (wet season) home range. Type C encounters (involving approach-retreat) may have been more frequent at the wells than elsewhere. It is likely that if the animals were dependent upon localized food sources the frequency of this encounter type would be higher. In this population there was no active competition between groups for food trees or sleeping sites. The order of progression in type E encounters
Possible determinants of the frequency of encounters.

- Size of home range.
- Length and pattern of day ranges.
- Extent of home range overlap.
- Density of habitat use (time and frequency in particular areas).
- Localized commodities — e.g. water.
- Group size.

Possible determinants of the nature of encounters.

- Whether or not the groups originated from a common group.
- Mechanism of group division.
- The extent of kinship between individuals in the different groups.
- Time since division.
- Proportion of different age-sex classes.
- Group size.
- The location of the encounter.
- Time since previous encounter.
- Major activity of individuals and the rate of group movement at the start of encounter.
- Personality of males involved in monitoring and tree shaking.
- Pugnaciousness of individuals, in particular adult and sub adult males.
- Personality traits of males and/or females which may partially determine group rank.
- The personality of individuals which lead or influence group movements.
- The outcome of previous encounters between the groups.
(essentially type C but with a long retreat) was probably an expression of the approach-retreat relationship between the groups. There is other evidence to show that locality influenced the encounter type. For instance, group 6 and 13 meeting on the western edge of group 6's home range had type E encounters. Elsewhere their encounters were type F.

Groups recently formed by the division of another group may have had a large home range overlap, a close knowledge of the individuals in each group and kinship with some members in the other group. This may explain the type G encounters and possibly, if division occurred longer ago, the type F encounters.

As in other macaques, adult and subadult males played a major part in encounters. They were involved in moving towards other groups, monitoring, tree-shaking and agonistic behaviour. The persistence and frequency of involvement of individual males in these types of behaviour may have affected the type of encounter. The repeated monitoring by the group 6 subadult males and one adult male from group 13 may have been partially responsible for the long type F encounters. Group 12 males seemed to monitor less than those of group 6 and there were no type F encounters between these groups. Since the rest of the group sometimes moved after the monitoring individuals the extent to which these individuals were followed by others may have influenced the encounter and in particular, the speed with which separation occurred. An individual's experience in past encounters probably influences its behaviour in subsequent encounters and consequently the overall performance of the group.

What is the function of monitoring behaviour? The term monitoring was used since males appeared to sit, observe and respond to movements by the other group's males. This knowledge of the other group's position might be particularly important if a relatively strange group was encountered. Presumably if groups met frequently, then individuals could predict, on the basis of previous experience, the probable behaviour of the other group's individuals. With strange groups, the males in the encounter zone may sense changes in the behaviour of the other group and would be the first individuals to respond. It is interesting to note in this context, the apparent reduction of monitoring during the later
phases of type F encounters. Also, when two groups united for the second time on one day (example 11), they did so without monitoring behaviour. These cases suggest that familiarity of the groups may be important in determining whether or not monitoring occurs.

There was little evidence for the exchange of males between groups in this study. Nevertheless this is known to be common in some macaque populations (Lindburg, 1969). It should therefore not be excluded as a possibility, especially when only a few days of detailed study were possible during the mating season. Intergroup monitoring might facilitate the exchange of males between groups by familiarizing the males of one group with those of another and by conveying information about the number and condition of males in other groups. A group with few males might be quickly indicated by a low level of monitoring behaviour. Marsden (1968 a) suggested that the frequent contact between peripheral rhesus males may facilitate group exchange.

When groups live in overlapping home ranges then they can be expected to meet on the basis of chance alone. Vessey (1968) considered that there was no evidence that groups actively sought each other out for encounters. When groups were some distance apart this applied to the study population. Once they were closer a definite attraction existed between some groups. Why did some groups meet and have lengthy encounters when complete avoidance would be possible? We know little of why home ranges have the shape and overlap pattern that they do. Encounters may not only familiarize individuals in one group with another (and so facilitate group exchange and permit group recognition), but may also play a major role in the spacing out of groups over the habitat. When home range overlap is imposed by ecological conditions then the extent of overlap might be adjusted by keeping encounters with identified neighbouring groups down to a minimum. When population density is high, encounters become more frequent and violent (cf Cayo Santiago studies). On Cayo Santiago this may be partially due to competition for food and Loy (1970) found a small, but non significant drop in the encounter rate when food was short. On an island, dispersal is impossible and the encounter rate is likely to be a function of group size, density and ranging behaviour. In the study population, tolerance between groups
would be expected to some extent during dry seasons when groups moved
to wells to drink. In territorial species encounters have a spacing
function and contain stereotyped components. Here, tree-shaking (see
Marler 1968) and intergroup monitoring were the most stereotyped
components of encounter behaviour. These elements may therefore be
the most important in maintaining the separation of groups and in
bringing about the ultimate dispersal of groups.

It must be emphasized that the classification used is a prelimin-
ary one. The heading given to each encounter type summarizes the
overall course of an encounter. In future studies it would be pre-
ferrable to analyse a larger sample of encounters using numerical
taxonomy techniques. This would test the overall validity of the
present classification and place any new classification on a more
empirical basis.

Addendum. Lindburg's (1971) more comprehensive account of intergroup
encounters in wild rhesus was seen after this chapter was completed.
His forest population showed some interesting similarities with the
population discussed here. Encounters occurred at a rate of 0.03
encounters/hr. Several different types were seen (but not apparently types
E and F) and the participation of subadult and juvenile males in an
intergroup monitoring-like behaviour was noted.

5.9. SUMMARY.

Intergroup encounters were varied in type but could be arranged
on a scale of increasing tendency for the groups to remain in each
other's proximity. The outcome of an encounter depended upon the
identity of the groups and possibly upon the context of the encounter.
The mean duration of encounters was 86 minutes. One group (group 6)
had approximately 0.05 encounters/hr. Many encounters occurred on the
edge of the group's core area. Approximately 50% of encounters included
overt agonistic behaviour between individuals from different groups.
Adult and subadult males played a major part in encounters. They partic-
ipated more frequently than other age-sex classes in the intergroup be-
behaviour which included tree-shaking, agonistic behaviour and intergroup
monitoring. The latter involved a decisive move by an individual towards another group, followed by a prolonged period of sitting and watching in the zone between the groups. In other macaques, adult and subadult males also play a major part in encounters. Several of the encounter types have been observed in other macaque populations. In provisioned populations the relative frequency of approach-retract encounters may be exaggerated by the localized resources. The results are discussed in terms of the wide variety of factors likely to influence the nature and frequency of encounters in this and other macaques.
6. FOOD AND WATER

6.1. INTRODUCTION.

In the study area the monkeys were entirely dependent on natural supplies of food and water. The animals were not provisioned or fed in any way. Only once were they seen to feed on man-supplied food; they rummaged among a patch of straw left by a camp. In other areas, where there was cultivation (e.g. Azrou), they were seen feeding in stubble fields and in some places (e.g. Tagounit and Ourika) we heard that they raided crops. Near Azrou they were also reported to feed on garbage. Owing to the seasonal climate at Ain Kahla the availability of food and water changed and the animals were forced to exploit whatever was available. Towards the end of the summer there were few green, herbaceous plants but a lot of new growth commenced with the autumn rains. Because of the low winter temperatures most plants did not flower and fruit until the following spring and summer.

With reference to the animals' food, my aim was to record its diversity, the techniques used to exploit items and to obtain some details of their seasonal availability. I believe (section 2.3.1) that the ability of this primate to live under very seasonal conditions, is closely related to its ability to efficiently exploit many different types of food from a wide variety of food plants. No measurements were made on the contribution of each species or each type of food item to the total diet.

During a brief period of the year the monkeys damaged the cedar trees by removing pieces of bark to feed on the phloem and cambial layers. This obvious damage makes the species a 'pest' with many of those concerned with the commercial exploitation of the forests. I have therefore taken this opportunity of assessing the relative importance of this damage when compared with other demands on the forests' resources.

The development of feeding techniques in babies and infants is discussed in chapter II.
6.2. METHODS.

When an animal was seen to eat a new plant species the location was identified and a sample taken. As the flowering season was brief and since flowering specimens were required for taxonomic purposes, those samples were pressed, dried and later matched against flowering specimens. A full collection of plants was maintained to ensure that flowering specimens were available to match against those discovered only after the flowers had finished. The specimens were deposited in the University of Leicester Herbarium and I am grateful to Professor T.G. Tutin for the loan of the flower presses and for identifying the specimens.

Faeces were collected during the late summer and winter. In order to discover what was available to the monkeys under the stones that they turned, samples of stones were turned in summer and winter. The monkey's success at finding items after stone turning was also recorded. Details of methods are provided in section 6.3.6.

6.3. THE SEARCH FOR FOOD.

6.3.1. Introduction.

Feeding was the animals' predominant activity and it took up a considerable part of the day. Its frequency and diurnal distribution in relation to other activities is discussed in sections 4.4.2. and 14.3. The movement of groups in relation to different parts of the habitat (where different food species were found) was discussed in sections 4.2.1. and 2.2.2. Most feeding took place on the ground, the trees being major sources of food during limited periods. In contrast to tropical habitats there was only a small variety of tree species that provided food. Six species were used and two of these were of minor importance. Items found on the ground were supplemented with fruits or other edible parts from the trees, as these came into season or when terestrial feeding was prevented by heavy falls of snow. While the monkeys did not rely upon the trees for all of their food the latter shows that the nutritional importance of the trees should not be underestimated.
The search for food involved a variety of techniques; digging with the hands, turning over of stones and fallen timber and the holding back of bushy shrubs to get to the bare ground underneath. Many items such as blades of grass, other leaves, seeds, flowers, some fungi and so on, were simply plucked or picked up from the surface using the thumb and first finger. In some cases only part of the item (e.g. the base of a stem) was eaten. When feeding from bushes or trees, the items were either bitten off directly (with or without the branch being pulled towards the animal) or the twig with the food item attached was pulled or bitten off and held to the mouth. On the ground the monkeys walked, picked up one or more items and then moved to another position and so on. When travel-feeding this movement from item to item tended to be unidirectional; when picking up several items they tended to sit.

Digging was used to pull bulbs, tubers, roots and fungi from beneath the surface and involved either the quick extraction of one item or more extensive excavations that occasionally covered several square feet. To dig, a monkey usually walked to the food item and started to dig (using alternate movements of both hands) in a semi-crouched position. It then sat down and continued to dig. Bulbs were quickly extracted but other items, such as roots, required considerable effort and the animal would move around the hole to dig from a different angle. The teeth were sometimes used to pull items from the ground. During digging and picking up items they shuffled short distances without standing. Direct competition between individuals for food items was infrequent; dyadic agonistic interactions over food items formed only an extremely small percentage of the total dyadic agonistic interactions. The nature of these interactions (based usually on a place where a monkey was digging or a food item such as a large fungus) and the possible presence of a more subtle, less direct form of competition affecting feeding efficiency is given in chapter 10.

The selection of individual food items from the surface seemed to vary from time to time and species to species. For instance while feeding on cedar seeds the animals often stood in one spot and picked up many seeds. While feeding on many plants
they would take one here, one there and then move off in spite of there being a high density of these plants around them. Cheek pouches were sometimes stuffed full and the food chewed later. These were most obvious in juveniles and infants that had little facial fur. Bouts of feeding and moving between feeding places were punctuated by other activities, such as resting, sitting and champing or interacting with others. Feeding bouts were also terminated by others approaching and initiating a social interaction.

Many food items were cleaned or manipulated before eating. With some species careful manipulation was required to obtain that part of the plant used for food. Items were usually manipulated and eaten where they were found; very occasionally, however, items were carried. Several methods were used; (a) holding the item in the mouth; (b) holding the item to the chest with one hand and moving on three legs; (c) holding the item to the chest with both hands and moving on the hind legs; (d) holding the item between the fingers but still (sometimes only every few paces) putting that hand to the ground. The items carried included fungi, large bulbs, leafy twigs, and pieces of hard packed snow. The greatest carrying distance observed was 30 m. Carrying was seen when a monkey that had found a food item moved to avoid the approach of another (5 instances), or when a monkey carried the item to a more comfortable spot before eating it (2 instances). For example, a monkey picking up a cedar twig on the snow carried it to a log protruding from the snow where he sat and ate the leaves. On other occasions there was no discernable reason for food carrying (5 instances). Under special, artificial circumstances (Frisch, 1960) food carrying in macaques can become extremely common. In M. sylvanus the basic behaviour patterns were present but infrequently used.

70 food plants were identified. This must, of course, be taken as a minimum since there were many occasions on which the item being eaten could not be identified. The species and the parts eaten are given in table 6.1.
TABLE 6.1. PLANTS EATEN BY MACACA SYLVANUS AT AIN KHALA

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>FOOD ITEMS</th>
<th>NOTES</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Leaves</td>
<td>Stems</td>
</tr>
<tr>
<td>GYMNOSPERMAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PINACEAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cedrus libanotica Link ssp. atlantica (Man.) Holmb.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>CUPRESSACEAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juniperus thurifera L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Juniperus oxycedrus L.</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>ANGIOSPERMAE - DICOTYLEDONES</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RANUNCULACEAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ranunculus calandrinioiides Oliver</td>
<td></td>
<td></td>
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<tr>
<td>Ranunculus rupestris Guss.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ranunculus paludosus Poir.</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>CRUCIFERAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Erysimum bocconei (All.) Pers.</td>
<td></td>
<td></td>
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<tr>
<td>Raffenaldia primuloides Godr.</td>
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<td></td>
</tr>
<tr>
<td>CARYOPHYLLACEAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stellaria media (L.) Vill.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>GERANIACEAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Geranium lucidum L.</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Geranium molle L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Geranium atlanticum Boiss. &amp; Reut.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>AQUIFOLIACEAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ilex aquifolium L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>PAPILIONACEAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vicia onobrychoides L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Medicago cf. falcata L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Species</td>
<td>Food Items</td>
<td>Notes</td>
</tr>
<tr>
<td>------------------------------</td>
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</tr>
<tr>
<td><strong>ROSACEAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rosa pouzzinii Tratt.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Geum urbanum L.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Geum sylvaticum Pourr.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Crataegus laciniata Moria</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><strong>CRASSULCEAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Umbiliclas rupestris (Salisb.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dandy</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Sedum album L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td><strong>SAXIFRAGACEAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saxifraga granulata L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td><strong>GROSSULARIACEAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ribes uva-crispa L.</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><strong>ARALIACEAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hedera helix L.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><strong>UMBELLIFERAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bunium alpinum Waldst.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>and Kit.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conopodium cf. Marianum</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Lange</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Torilis arvensis (Huds.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Link</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thapsia villosa L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td><strong>POLYGONACEAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rumex ? ginii Jahand.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>and Maire</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>FAGACEAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quercus ilex L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td><strong>SCROPHULARIACEAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Veronica hederifolia L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td><strong>LABIATAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clinopodium sp.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><strong>RUBIACEAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Galium cf. apanis L.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>SPECIES</td>
<td>FOOD ITEMS</td>
<td>NOTES</td>
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<tr>
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</tr>
<tr>
<td><strong>DIPSACACEAE</strong></td>
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<td></td>
</tr>
<tr>
<td>Valeriana tuberosa L.</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td><strong>COMPOSITAE</strong></td>
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<td></td>
</tr>
<tr>
<td>Bellis sylvestris (L.) Cass.</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Centaurea nana Desf.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Centaurea puliata L.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Carduus sp.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Cirsium echinatum (Desf.) DC.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Crepis vesicaria ? sep stellata (Ball) Bab.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Andryala sp.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Microlonchus salmanticus (L.) DC.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Picnomon acarna (L.) Cass</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Cymara hystrix Ball</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Chamaepeuce casabonae DC.</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Catananche caerulea L.</td>
<td>X</td>
<td>X (4)</td>
</tr>
<tr>
<td><strong>ANGIOSPERMAE - MONOCOTYLEDONES LILIACEAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ornithogalum comosum L.</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Tulipa sylvestris L.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Muscari grandiflorum Baker</td>
<td>X</td>
<td>(5)</td>
</tr>
<tr>
<td>Muscari comosum (L.) Miller</td>
<td>X</td>
<td>(5)</td>
</tr>
<tr>
<td><strong>IRIDACEAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crocus nudiflorus Sm.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Crocus nevadensis Amo and Campo</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Romulea bulbocodium (L.) Seb. and Mauri</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><strong>GRAMINEAE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Helictotrichon jahandiezii (Litard.) Potzstal</td>
<td>X</td>
<td>(6)</td>
</tr>
<tr>
<td>Cynosurus elegans Desf.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Agropyron panormitanum Parl.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Bromus tectorum L.</td>
<td>X</td>
<td>(7)</td>
</tr>
<tr>
<td>Bromus sterilis L.</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>

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*Note: The table represents a list of plant species, some of which are mentioned under different botanical families. The 'X' marks indicate the presence of a species within a family.
<table>
<thead>
<tr>
<th>SPECIES</th>
<th>FOOD ITEMS</th>
<th>NOTES</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>Festuca triflora</em> Desf.</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>2. <em>Vulpia geniculata</em> (L.)</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>4. (Font Quer and Pau) <em>Meld</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. <em>Festuca paniculata</em> (L.) Schinz and Thell. var. <em>baetica</em> (Hack.) Maire and Weiller</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>6. <em>Poa bulbosa</em> L.</td>
<td></td>
<td>X</td>
</tr>
</tbody>
</table>

**OTHER FOOD PLANTS**

**LICHENS**

- *Pseudeveria furfuracea* (L.)
  - *Zopf var furfuracea*
- *Letharia vulpina* (L.)

**FUNGI**

A minimum of 5 unidentified species.

**NOTES.**

1. Also ate cotyledons, stem of germinating seedlings, cambium, phloem and (rarely) bark.
2. Petiole and pedicel only.
3. Pedicel.
4. Tips of leaves eaten.
5. Peduncle of inflorescence only.
6. Part of stem eaten is short, bulbrous, basal internode.
7. Leaves scraped.

The roots of *Anthyllis vulneraria* L. were eaten at Tagounit. This species was also found at Ain Kahla.
6.3.2. Food from cedar trees.

Fig. 6.1. shows the seasons during which various parts of the cedar trees were eaten. Cedar leaves were principally eaten from early November through towards the end of February. The cedar leaves were, of course, present throughout the year and the new growth that one would expect to be most suitable for consumption started with the autumn rains. Growth, while proceeding throughout the winter, did not reach a maximum until the spring when the trees had long green shoots. Observations showed that in the autumn and winter they were not concentrating on the new growth, but were taking both old and new leaves. Indeed the new growth available during the autumn and winter was much less than that available during March, April and May when they did not feed on cedar. Feeding on cedar leaves was predominantly seen during the early morning, mid-day and evening when they were more often in the trees. During the rest of the day they fed on other plants, only occasionally taking cedar leaves. After heavy snow falls, when most other plants were unavailable, they ate little else besides cedar (section 6.3.7). Once the snow melted they returned to other plants. It seemed as if they preferred not to feed on cedar leaves when other food was available.

It is possible that they could only consume cedar leaves when they had sufficient water. In the late autumn and winter there was plenty of water available, but during the spring of 1969 the eating of cedar leaves ceased when the weather became dry. It was subsequently seen in isolated incidents on nine separate days (fig. 6.1); on each occasion there had been rain after a period of very dry weather. Cedar leaves occurred regularly in their faeces in winter, but not in summer.

When eating cedar leaves they pulled off the small leaf clusters with their incisors or fingers, held them in the hand and bit at them. Twigs were bent up from the tree and the leaves removed or the twig broken off and held to the mouth. They usually fed in trees with pyramidal and not flattened tops. Although they tended to feed in the tops of the trees they were never seen to break

* See Deag (1970).
### FIGURE 6.1.
Seasonal distribution of feeding behaviour on *Cedrus labonotica atlantica*. Based on data from Ain Kahla, 23.7.68 to 7.10.69.
off the leading shoot. They did not usually feed in very young trees (<6 m.) or those just sprouting out of the ground. Sometimes, particularly during snowy periods, they fed on the ground by picking up cedar twigs dropped by other monkeys feeding above. During very cold weather and blizzards they sat with their hands held to the chest and just leaned forwards to bite off the leaves.

**Cedar seeds.** When the cones were ripe and disintegrating in the autumn and winter, the monkeys ate the seeds. Most seeds were picked up from the ground but they also picked the seeds out of the cones still on the trees, or pulled these off and dismembered them with teeth and fingers.

**Cedar seedlings.** The monkeys continued to feed off the seeds once they had rooted and also ate the young seedlings with cotyledons. They pulled up the seedlings with one hand, pulled off the testa and dropped it with the other and then, putting the seedling to the mouth, they bit off the cotyledons and upper stem. The lower stem and root was discarded. Another technique was to pull up the seedling with one hand, put it root first into the mouth and hold it with the teeth while removing the testa. The whole seedling was then taken into the mouth. Once the seedlings had shed the testa, the cotyledons matured and new clusters of leaves formed, the seedlings were not eaten by the monkeys. Nibbled seedlings, still rooted in the ground, with part or all of the cotyledons removed appeared to be a result of sheep grazing.

**Cedar cambium and phloem.** The monkeys removed the bark with the cambium and phloem attached and then peeled off and ate these soft tissues. Only once was a monkey seen to eat the bark. In that instance the bark was the smooth, silvery type seen on young stems. The monkeys bent down towards the bark and pulled off pieces with their incisors and, less frequently, their fingers. The bark was then held in the hands, the soft tissues pulled off with the teeth and the bark dropped to the ground. Monkeys, often returned to places where bark removal was started earlier in the day by themselves or other animals. Presumably it was easier to continue working in one spot than to start a new one.
Bark was usually removed from trees taller than about 6 m. One reason for this may be that, as with leaf eating, the monkeys were in the trees for other purposes (e.g. sleeping or resting) and did these activities in the larger trees. The monkeys concentrated upon the light and medium grade barks; the really thick, coarse bark of the main trunk of fully mature trees was not removed. They often fed in one place on bark for at least half an hour. A few young trees were seen to be stripped and this is apparently more frequent in at least one other forest (section 6.5). Bark stripping completely around the stem or branch resulted in the death of the tree distal to that point.

Cedar male strobiles. The male flowers were eaten when they were young, green and tender; once ripe and full of pollen they were ignored. They were pulled off with the fingers or teeth. They probably also ate the female strobiles (young cones) which appeared at the same time. These were, however, less numerous and difficult to separate from the male cones at a distance.

These food items from the cedars were resinous. It is unknown whether the monkeys have any special alimentary adaptation to handle this type of food. Also taken from cedar trees were the two species of lichen. These were chiefly eaten during the late summer, autumn and winter.

6.3.3. Food from other trees.

The remaining trees in the forest were all food plants but only three, *Quercus ilex*, *Juniperus thurifera* and *Crataegus laciniata*, were of major importance. *Juniperus oxycedrus* and *Ilex aquifolium* were rare; there were probably no more than a dozen of each in the study area.

*Quercus ilex*. The monkeys ate almost no mature oak leaves; only the occasional bite was seen. Infants pulled them off and bit them during play. Young shoots and leaves were eaten in small quantities during the spring and summer. The monkeys fed more on the caterpillars
that fed on the leaves, than they did on the leaves themselves. The summer and autumn of 1968 was a poor fruiting season and there were few acorns. In 1969 there was a heavy crop and from August until the end of the study, acorns were a major food. Most were picked or bitten from the trees, (or from twigs that had previously been snapped or bitten off), but some were picked up from the ground. Before eating the kernel the cup and sometimes the seed coat were removed. Either the whole acorn was put into the mouth and the cup and seed coat removed using the teeth (with or without holding it by the fingers) or they held the acorn up to the mouth and bit off the lower third of the cup with the incisors before removing the seed coat and the remaining part of the cup. (See plate 6a, b and Drag, 1970)

**Juniperus thurifera.** The juniper 'berries' were ripe in early September and there was fruit on some trees until early the following March. The monkeys ate the fleshy outsides of the berries. They were picked individually by the fingers or the mouth, either directly from the tree or from a twig that had been broken off. Only one berry was put into the mouth at a time and it was held between the first finger and thumb and bitten at with the teeth. The berry was occasionally removed, examined and manipulated again before the kernel, stripped of its fleshy covering, was dropped. The monkeys also ate the leaves and the male strobiles. The larger 'berries' of *J. oxycedrus* were ripe at about the same time and eaten in much the same way.

**Crataegus laciniata.** The deciduous hawthorn produced new leaves in May and June. Both old and new leaves were eaten. The fruits, ripe and available from September to November, were completely eaten. To reach a fruit on the end of a slender branch, the animal either stood bipedally on the ground and pulled the branch down or sat in the tree and pulled the bough towards it. Fruits and leaves were either bitten or pulled off singly and several were chewed at one time.
6.3.4. Other plants.

The eating of grasses provided an interesting example of the variety of food obtained from one family of plants and how feeding techniques were suited not only to the parts of the plant being eaten (which is related to the season), but also to the anatomy of each species.

Following the autumn rains a fresh growth of grass occurred in most of the study area. Young blades were picked with the thumb and first finger either of one hand or both hands used alternatively in a regularly repetitive action.* While several leaves were often picked together there was no bunching of items as seen, for instance, in Theropithecus gelada (Crook and Aldrich-Blake, 1968). Eating grass in this fashion continued as long as fresh growth was available - i.e. throughout the winter, spring and early summer. At other times of the year fresh grass was seen only in the damper areas, for instance around the wells. The softer parts of larger grass leaves (e.g. those of Bromus sterilis) were scraped off by drawing them through the teeth. Helictotrichon jahandiezii was pulled up and the bulbule at the base of the stem bitten off.

During the summer, grass seeds formed a major food. These were removed from the stem using a variety of techniques that differed with the anatomy of the grass:

With Poa bulbosa, Festuca triflora, Vulpia geniculata, all light, 'feathery', grasses the seed heads were pulled through the teeth and the seeds extracted. With Cynosurus elegans, a more lightly rooted species, the plant was uprooted and held to the mouth.

In the coarser grasses Agropyron marginatum and A. panormitanum the seeds were harder to remove since the seed heads are more heavily built and the spikelets containing the seeds closely attached to the stem. Without uprooting the plant they drew the seed head through the mouth, often guiding it with the other hand, held it up to the mouth with both hands and bit the seeds off or pulled the seeds off with the fingers and placed them to the mouth.

* Plate 61d.
In *Bromus sterilis* and *B. tectorum* the spikelets hang down on pedicels and on some occasions the seeds were removed with a technique which ensured that the seeds were freed of their pedicels. The stem was held with one hand and the other pulled up it. This removed the seeds in a clump and left them in the palm of the hand with the pedicels, still attached to the seeds, pointing out of the hand. The pedicels were gripped with the fingers of the other hand, the seeds bitten off and the rest dropped to the ground.

Towards the end of the summer there was little green, herbaceous vegetation and the monkeys pulled up the dead grass plants by gripping the short, dead stem. After pulling the plant through the fingers to remove the soil and roots, the small slightly swollen base of the leaves and the stem was eaten and the dead leaves dropped to the ground.

Thistles were another group of plants which required careful manipulation to get at the edible parts. Five species were known to be eaten. Early in the year other parts were eaten, but during the late summer they extracted the seeds. To obtain the seeds from the tough, spiny species (e.g. *Picnomon acarna*, *Cirsium echinatum* and *Cynara hystrix*) the monkeys sat by the plant, leaned towards it and gripped the matured florets in the teeth. With *Picnomon acarna* the flowers were occasionally held. The monkey then pulled back extracting the florets with the large seeds at the base. The florets were then either held in the hand and the seeds bitten off, (*Picnomon acarna*) or they were held in the hand or put on the ground and sorted through before the seeds were eaten (*Cynara hystrix*). Holding the plant was more common with *Chamaepeuce casabonae* and with this species they extracted the seeds by pulling at the flowers with the fingers.

The monkeys dug for bulbs, roots and tubers in all seasons. During travel feeding numerous little scoops were left as the animals dug for separate items. As travel feeding slowed down, these became more frequent and they made larger excavations. Many of the single scoops were obviously aimed at a particular plant and the aerial parts were left lying after the bulb or tuber was eaten. Larger excavations seemed to be more haphazard — in as much as there were no aerial parts of the plant showing above the turf. Items
removed from the soil were almost always cleaned before eating. Bulbs were held in one hand and then the teeth used to peel away the outer leaves. Roots and tubers were pulled between the fingers to brush off the soil. The end of the root would be held in one hand and pulled through the fingers of the other. At the last moment these would grip the root and the first hand would let it go. The process was repeated, the root changing from hand to hand with its whole length being cleaned of soil. Roots were not peeled.

Fungus was available during all except the dryest seasons. They were dug from the soil and cleaned as above or more simply by brushing the surface with one hand.* They either ate the whole fungus or left the outer surface of the pileus. Some were collected from holes inside trees.** Fungi that were unearthed or picked were not always eaten. After being brought to the face they were dropped. This applied especially to many of the brightly coloured species.

Loose soil and leaf litter were brushed backwards and forwards with the hands and followed with the eyes. Items, too small to be identified, were then picked up.

6.3.5. Stone turning and animal food.

Plants provided the bulk of their food, but they were also seen to eat some animals. They probably ate many more which, because of their small size, could not be seen. As the monkeys moved through the forest or along the forest slopes they repeatedly turned over the numerous stones found there.*** These ranged in size from small pebbles that were flicked over with the fingers to larger rocks that were pulled with both hands and required considerable effort. Stones that had been turned sometimes rolled down the slopes and this may have contributed to the legends that the monkeys throw stones at people. Both plants and animals were found under the stones. It was difficult to prove that animals were being eaten; however, they were seen to pick objects from the undersurfaces of the stones and to eat scorpions and once a snail. Occasionally animals gave startle reactions as they turned a stone but the cause of this was never discovered. Plants under stones were easier to see and they occasionally bent down and pulled at items with the teeth.

* Deag (1970); ** plate 6.1 e, f; *** plate 6.1 c and Deag (1970).
(a) A juvenile male feeds on *Quercus ilex* acorns (JM1, group 6).
(b) An adult male bites at an acorn in order to remove the cup (AM3, group 6).
(c) An adult female (in moult) stone turning (AF4, group 6).
(d) A subadult male feeding on blades of grass. Note the action involving alternate use of both hands to pick up items and put them to the mouth (SM1, group 6).
PLATE 6.1 (contd.)

(e & f) A subadult male gathering fungus from a tree hole (SM2, group 6).
In order to investigate what was available under the stones, 400 stones were turned. These were divided equally between summer (3.6.69 and winter (7.1.69), and between the slopes and forest (pure cedar and oak with cedar sampled). Only stones that had not been recently turned were examined, but it is not known whether the monkeys made a similar decision. The results for animals found under the stones are given in table 6.2. The animals found included white, brown and black ants (Formicoidea), scorpions (Scorpionidea), wood lice (Isopoda), spiders (Araýeida), millipedes (Diplododa), centipedes (Chilopoda) earwigs (Dermaptera) snails (Gastropoda), beetles (Coleoptera) and various larvae and cocoons. They were all found in both seasons except for wood lice, snails and earwigs which were not recorded in the summer. A chi-square test (table 6.2), showed that the proportion of stones with animals under them did not differ significantly with either the season or the position of the stones. The ground under stones turned in the winter was damp and most of them (exact numbers not recorded) had small fresh shoots or etiolated leaves under them, with fewer in the forest part of the sample. In the summer sample only 18 (10 slopes, 8 forest) were found to have shoots. The ground under these stones was dry. We can conclude that while there was no difference between summer and winter with reference to the number of animals available the number of plants available was much higher in winter.

In a parallel investigation I recorded the success of the monkeys while turning stones. Unfortunately it was not possible to match the samples exactly. In the summer (30.8.69 to 2.9.69) 200 stone turnings, equally distributed between slopes and forest, were recorded. In the 'winter' (25.1.69 to 2.3.69) 74 stone turnings were recorded; all on the slopes. Their success at obtaining items varied with the season; items were picked up from under 67% (50/74) of stones in winter and 15% (15/100, slopes, 15/100 forest) of stones in the summer. Their success in winter was therefore much higher than the number found to have animals under (25%). This seems to show that stone turning in winter was rewarded by a higher proportion of plant finds. Their success in summer was lower than the proportion with animals (27%) but higher than the proportion with plants (9%). The stone turning habits of these
### Table 6.2: Results of Stone Turning by the Observer

<table>
<thead>
<tr>
<th></th>
<th>Forest</th>
<th>Slopes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer</td>
<td>32* (40)**</td>
<td>27 (35)</td>
</tr>
<tr>
<td>Winter</td>
<td>24 (38)</td>
<td>27 (43)</td>
</tr>
</tbody>
</table>

* Number of stones out of 100 that had animals under them.

** Total number of animals found under the stones. (Ant nests counted as one 'animal').

\[ X^2 \text{ (With expectation derived from margin and grand totals)} = 0.56 \]
\[ df = 1. \text{ Not significant at 5\% level.} \]
(and other ?) monkeys should probably be looked at as part of a general search for food items rather than as a specific search for animals. It could be, however, that the monkeys need to turn stones to obtain a particular fraction of their diet and the presence of succulent shoots is an added 'bonus'.

Grasshoppers (Orthoptera) were eaten. The seated or standing monkey repeatedly lashed out or pounced on them. Flies that settled by infants and juveniles were also chased and swatted but it is unknown whether those were eaten. On one occasion a monkey ate an unidentified species of lizard.

The eating of caterpillars. During July 1969 a heavy infestation of caterpillars was observed on the Quercus ilex trees. This may have been present during mid and late June when the observer was absent from the study area. During July, the monkeys frequently fed in these trees which had previously been virtually ignored. Observations showed that, while a few young leaves were eaten, their major quarry were the caterpillars.

Methods of catching. Two techniques were used to catch the caterpillars: (a) The monkeys either sat, scanning the leaves, fixated on a caterpillar and then moved to pick it up, or moved through the branches (or over the ground in the case of low branches) reaching out and picking off the caterpillars. Each caterpillar was eaten before the next was picked up. (b) The caterpillars had a startle reaction and when touched they dropped from the leaves to the ground. Monkeys moved under the trees, where they or others had been feeding, and picked up those that had dropped.

Methods of eating. Two techniques were used to eat the caterpillars: (a) The caterpillar was gripped at one end with the fingers and pieces bitten off and chewed. (b) The caterpillar, held as above, was put to the mouth and pulled like a piece of elastic between the lips and/or incisors. When repeated several times this extracted the insides. The skin was then eaten.

Before the eating of caterpillars commenced, the monkeys' faeces were dark green; while eating them they were red-brown.
The fur around the mouth became moist and stuck together with the juices. The caterpillars (sp. indet.) were ca 4 cm. long, thick and with grey-brown dorsally and yellow ventrally.

The eating of scorpions. Scorpions (Buthus occitanus - probably B.o. tunetanus var. Lepineyi Vauchon) were frequently seen beneath rocks both on the edge of the forest and on the slopes and spurs. An animal turned over a rock and revealed the yellow-brown scorpion. On exposure this scuttled around and the monkey chased it with its hand and made attempts to catch it using the thumb and first finger. During these attempts the hand was pulled smartly away from the scorpion repeatedly. It was finally caught and bitten several times. (During one incompletely observed sequence the monkey was seen to jump high and to the side. Sitting down, it brought its right hind foot up to its mouth and licked it). Examination of the area near the turned rock revealed the scorpion's hole, where it had been hidden under the rock, and the scorpion's post-abdomen (tail with terminal sting) bitten off between the second post-abdominal segment and the pre-abdomen. It is assumed from this, the way the monkeys chased the scorpion and the way it squirmed around while being brought up to the mouth, that the monkeys caught the scorpion by the post-abdomen from behind.

6.3.6. Feeding during snowy periods.

During snowy periods the monkeys were forced to modify their food searching habits. After light falls, most animals fed in clear patches but a few scraped away the snow where it was less than perhaps 6 or 7 cm. deep. Even after heavier falls there were usually clear patches under trees or in the shelter of large rocks. Snow melting from a tree soon left a clear patch on the ground under the canopy. The monkeys therefore moved from the base of one tree to another pausing at each to pick up food items. Stone turning was also used to reveal clear patches where they dug or picked up items. They also used the south facing slopes (where the snow was first melted) or places from which the wind had blown the snow.
After heavier falls, for instance when there was a complete covering of 30 cm. or so of snow, the animals' feeding habits changed markedly. During most of the winter, cedar leaves were included in their varied diet but under these conditions they were (save for lichen) their sole food item. Most of the day was spent in the trees and they descended only to move from tree to tree. Eating cedar leaves during snowy weather was accompanied by major problems. Frosts usually followed the snow melting and each night the cedar branches and leaves were encased in thick ice which the observer at least found difficult to remove. There were also icicles hanging from the branches and snow piled on the boughs. Under these conditions the trees were hazardous and the monkeys were seen to slip. As the sun reached the trees the ice melted and (if it was a sunny day) the monkeys tended to feed in these trees that had the sun on them. In severe winters, icing is probably a major problem. During the winter 1968-69 pure cedar eating (plus some lichens) probably did not last for longer than four or five days, since the snow rapidly melted to leave clear patches under the trees.

Whiten (1972 and personal communication) reported that in the Rif 7-10 cm. (3-4") of snow made feeding on the ground impossible and that all feeding then took place in the trees. At Bab Taza there were no cedars and the monkeys were seen in junipers and oaks.

6.4. WATER.

6.4.1. Availability.

Water availability was closely related to rainfall (section 2.2.3) and within the study area there were only two permanent sources of water available to the monkeys (section 2.2.1). The spring in the centre of the main bled, 0.5 km. from the forest, was never visited. Owing to the porous rock there was little surface water at Ain Kahla and any temporary pools were small. The most long lasting were found on the road where the soil was compacted. A stream ran through part of the forest but it only carried water for a few days after a period of rain or when the
snow was melting. Towards the end of the summer and early autumn the habitat was extremely dry and there was little, if any, (see below) water available away from the wells. With the autumn rains, water became abundant everywhere and collected in temporary streams and pools, pools in rocks, tree stumps and holes in trees. Throughout the winter repeated falls of rain and snow replenished these temporary sources from which the monkeys drank. Those groups that had a well within their home range visited it throughout the year but they drank less often in the winter when it was cooler and water was picked up with their food. In the summer they drank on most days if they had a well in their range.

From March 1969 (when the temperature was increasing, Fig. 2.4) there were longer periods without rain (Fig. 2.5). In these dry periods the temporary sources of water repeatedly dried up or almost did so. The most resistant to drying up were the holes deep within the trunks of cedars and oaks. Whether or not these temporary sources dry up completely probably depends upon the temperature and distribution of rainfall in each summer and autumn. During 1969 group 6 were able to find water in their home range throughout the summer and autumn. There were several trees with water holes in them and these were repeatedly visited. The monkeys were not observed to drink every day but it is highly likely that I never discovered all of the water holes that they used. In mid August after 36 days with no more than a trace of rain (fig. 2.5) almost all of the holes were dry and the monkeys were seen to try several holes without success. A hail storm then provided hail to eat and rain replenished the temporary water. Dew occurred intermittently throughout the summer although not always in the forest which was warmer at night.

The summer and autumn of 1968 were extremely dry (Fig. 2.5). The ranging patterns of several groups, and the fact that group 6 was then seen outside its main home range, suggested that the temporary sources of water dried up completely and that all groups were forced to move to the permanent supply at the wells (section 3.4.2).
6.4.2. Drinking techniques.

Several methods were used to obtain water from the above sources. At the wells or temporary pools the animals crouched or bent down to drink. The cautious approach to water sources in the open is discussed in section 7.3.3. When rain fell after a dry period, the animals moved from rock to rock and drank from the small puddles or licked the rain from the vegetation. Boughs were pulled down and water drops licked from the tips of twigs. When hail fell after 36 days without rain they rushed around picking up the first hail stones and eating them. As more fell, they sat in one spot and picked them up.

In the spring, when there were a few snow patches remaining on north facing slopes, the monkeys approached and licked them or broke off snow and ate it. Whiten (1972) recorded similar behaviour in the Rif but following the first snow fall of the winter.

To drink from a hole in a tree stump or trunk or from a small trickle of water on the ground, they frequently used an indirect method when the water was too low to drink normally. The face was placed near the hole and turned to the side. The hand was repeatedly dipped in and brought up to the face to run water into the mouth. When there was less water in the hole they licked their hand and fingers. If the water was deep within a trunk the body was positioned carefully so as to dip the arm deep inside it. Some holes were so deep that only the larger individuals could reach the water; others were so small that only the smaller individuals could get their hands in. Monkeys sometimes passively avoided others approaching to drink or were threatened away from the hole; they left or waited before moving in to drink again. Often several monkeys sat around waiting their turn. In group 6 agonistic behaviour over water positions formed a minute fraction of the total agonistic behaviour (chapter 10). It is unknown whether such behaviour is more common when the monkeys drink in the open at the wells.
As the monkeys fed on the cedars it is important here to comment on any damage that they did and to assess its significance in relation to other demands on the forest's resources.

The loss of seeds, germinating seedlings and male strobiles probably has little effect on regeneration since they are produced in huge quantities. The eating of cedar leaves is not thought to stunt the growth of the trees since the monkeys were not seen to concentrate on the terminal shoots. The removal of bark was the most obvious and probably the most destructive of their cedar eating habits. The loss of side branches and the occasional removal of bark from the main stem of younger trees must result in a loss of timber. The monkeys at Ain Kahla, however, only removed the bark during two months of the year and their habit of repeatedly returning to one branch localized the damage. Even in that season cedar was, of course, only one component of a very varied diet. Compared with the other losses of timber from the forest (official felling, large losses of immature timber caused by felling operations, illegal felling by shepherds) these losses are probably extremely small. They may, however, assume economic 'importance' simply because man, in over-exploiting the timber, feels that other losses must be kept to a minimum.

It is my opinion (admittedly based on only a short period in the forest) that the regeneration of cedar at Ain Kahla is not keeping up with exploitation. The factors controlling regeneration are extremely diverse and depend very much upon a suitable balance of temperature, humidity, minerals, fungal mycorrhiza and so on (Marion, 1953-55; Lepoutre, 1957-61, 1962-63; Pujos, 1964). Reduced regeneration may be a direct consequence of the exploitation rate and methods. The removal of significant numbers of mature cedars and oaks may upset the temperature and humidity balance at ground level. On calcareous soils the seedlings are very susceptible to drying out in the spring and in some areas this will be exaggerated by loss of shade. Immature trees, already established in felling areas, are often destroyed during felling operations and during the carting of timber. The grazing of sheep and goats in
the forest also severely limits the establishment of new trees. This appears to be the least studied aspect of cedar regeneration.

The monkeys did not browse on the seedlings once the cotyledons had opened out. In their extremely selective feeding these were not touched. This was in marked contrast to the sheep (and the few goats) that grazed in the forest. During 1969 the sheep were excluded from the forest and bled until June. Only one or two weeks after the sheep arrived there was a drastic change in the vegetation. This was beaten flat in wide bands; paths created by the passage of flocks of ca. 200 sheep. They were not selective feeders. It seemed as if the moving flock ate more or less anything in its path. The sheep browsed on the lower cedar branches and at the end of the summer, when pasture was poor, the shepherds lobbed off side branches or even felled tall trees to feed them. It is therefore unlikely that young seedlings escaped being eaten. The adverse influence of grazing animals and the minimal damage caused by seed eaters on the regeneration of forests is recognized for other trees (Mellanby, 1968). The shepherds realized that they were over exploiting the pastures; many of them moved on after a month or so, leaving a smaller density of sheep in the valley. For herbaceous plants the longterm damage due to summer grazing by sheep was probably small. Most annuals had dropped their seeds before grazing commenced and perennials had subteranean bulbs and tubers. Grazing must, however, reduce the food available to the monkeys during the summer. The only other major herbivours in the forest were pigs, hares, small rodents and birds. These must compete for some food items but, compared with the huge biomass of sheep, cattle and goats, their effect on the herbaceous vegetation is probably small. One food plant, a lichen (Pseudeveria furfuracea) was collected in considerable quantities for export to France.

In the Assaka-n-ouam cedar forest (N.E. of Bekrit) the damage by monkeys was said to be more extensive with very young trees being heavily damaged by bark removal (Arnaud, personal communication). This forest is a small (ca 21 sq.km.) isolated one and it would be of interest to compare it with Ain Kahla in order to determine the reason for this damage. It may well be related to population density and the availability of other food. It is
essential that extensive data on population density, damage to trees etc. is collected before any attempt is made to control the number of monkeys in the Moroccan forests. For instance during 1969 ca 120 monkeys were caught in the oak forests near Azrou for export to Alsace, France. In an oak forest the monkeys do almost no damage and their caterpillar eating may be beneficial. From the forester's point of view these monkeys should have been caught in places like Assak-n-Ouam where damage to cedars is known to be important.

As the forests have been traditional grazing grounds for generations (Metro, 1958) it is difficult to control grazing. Much grazing is however carried out by employees of people who no longer move with the flocks. This may be one factor producing the high densities of sheep. Perhaps regeneration could be promoted by restricting grazing in some parts of the forest for several years at a time and by restricting the number of sheep in the whole area.

The monkeys have been there for even longer and it is to be hoped that man, in his search for an instant cure to his economic problems, will not see fit to destroy them. Quite apart from any moral, ecological, scientific or medical arguments (Southwick et al, 1970) that can be put forwards for their preservation they represent an important natural resource. With an increase in leisure time available to the Moroccan people and the increasing number of tourists visiting their country these monkeys may be appreciated as a major economic asset.

6.6. SUMMARY.

The monkeys studied were entirely dependent upon natural food and water and there was little direct competition between individuals for food items. Most feeding took place on the ground, the trees (chiefly cedar, holm oak, juniper and hawthorn) being major sources of food during limited periods. 70 food plants were identified and details of the parts eaten are given. The monkeys were catholic both in the variety of species eaten and in the parts consumed. Many items were seasonal and their diet varied considerably throughout the year. Cedar leaves, for instance, were eaten from November
through February; cedar seeds from December through February; cedar seedlings from March through May, cedar cambium and phloem in May and June and the male flowers of cedar in July and August. Many food items required considerable manipulation and the techniques used to exploit the plants were related to the anatomy of each species. For instance grass seeds were removed by pulling through the mouth, the fingers or by biting at the seeds and the technique used could be related to the anatomy of the seed head. The cleaning or peeling of items obtained from the soil was also noted. Food items were usually eaten where they were found.

Plants provided the bulk of their food but they also ate animals. Stones were repeatedly turned and animals and (particularly in winter) young, fresh, etiolated shoots and leaves were found and eaten. Scorpions, found beneath the stones, were eaten except for the tail and sting. Other animals known to have been eaten included grasshoppers, caterpillars and (only once each) a snail and lizard. After heavy falls of snow they fed almost entirely in the trees on cedar leaves and lichen.

There were only two permanent sources of water in the study area and these were not included within the main home range of some groups. They drank from small temporary water holes (in rocks and tree trunks) and in the dry season these were periodically replenished with the occasional rain or hail fall. Contrasts in the movement of groups in 1968 and 1969 suggested that in some summers the temporary water holes dry up and that all groups are then forced to move to permanent sources of water. Water was usually drunk directly but they also ate snow, licked vegetation and dipped their hands into water in inaccessible places.

The monkeys damaged the cedars by removing the bark to get to the cambium and phloem. Compared, however, with other demands on the forest the resulting loss of timber must be extremely small. Although they ate the cedar seeds and germinating seedlings they did not damage rooted seedlings older than the first cotyledon stage; the sheep grazed in the forest were, however, extremely unselective feeders and were known to eat cedar leaves. When compared to the damage to regenerating trees caused by man and sheep, the damage caused by monkeys removing bark should not be exaggerated.
7. RESPONSES TO PEOPLE, PREDATORS AND OTHER ANIMALS

7.1. INTRODUCTION.

Since I wished to record the undisturbed and natural behaviour of the animals it was essential to recognize the occasions on which the behaviour exhibited was a result of my presence. An observer must have been a strange phenomenon for the monkeys; in contrast to them seeing people only occasionally and for short periods of time, I moved with them from sunrise to sunset. Eventually group 6 became more or less habituated and close observations were possible without disturbing the monkeys. By 'habituated' it is meant that the animals ceased to react to my presence in the way that they did to other people.

The methods used to make observations have been given in section 1.42. Basically the observer attempted to be neutral, interacting neither positively nor negatively with the animals. While the group 6 monkeys became habituated to the observer, this did not affect their relationship with other people, showing that they could, in some way, distinguish between them.

The presence of people or animals sometimes influenced the direction and speed of a group's movements. This has been discussed in section 4.2.4.

7.2. RESPONSES TO THE OBSERVER AND OTHER PERSONS.

A variety of responses were due to the observer's presence. Several were seen when other people or predators were also present and most of them probably occurred under those circumstances. Tree-shaking at the observer was included in section 5.6.1.

7.2.1. Fleeing and hiding from the observer.

When the observer was on foot the flight distance varied unpredictably from 60 m. (and occasionally less) to 200 m. (Flight
distance was the distance at which the animals fled from the observer. It was lowest when the monkeys were near the roads and tracks. If the observer moved or stood quietly in the open at least 60 m. from the group they usually paused, looked towards him and perhaps moved off. If there was an element of surprise or uncertainty, or if the observer was moving rapidly towards the animals, a bark or series of barks was almost always given. Following this call monkeys feeding outside the forest ran towards the forest and partially ascended the nearest trees or stood under them. In the forest they ascended the trees directly. Animals that did not flee following a bark or fled but did not ascend the trees, looked around in an alert manner. Barks were given in bouts of variable length and intensity (section 3.2.9). A single vigorous call or a bout of vigorous calling was almost always followed by flight. Single, low intensity calls were followed either by flight or by a reduced action such as jumping up and looking around. Responses to barks varied with age-sex class; adult males often continued to feed in the open while others ran for cover.

The initial flight to the trees was followed by various actions. When I moved away or sat quietly in the open at least 60 m. distant, the animals usually descended within five minutes, continued with their previous activities and often moved slowly away. On the edge of the forest they would move down from the trees and feed in the open, occasionally glancing at the observer. When I moved slowly closer after their initial flight, they descended rapidly (even at 20 m.) or climbed through the trees before descending and running away over the ground. They sometimes did this if I moved away from them - especially if they were close when first disturbed. Animals in trees separated from the forest descended and ran swiftly to the forest. If I moved rapidly towards the trees they ascended to the top and hid. The monkeys frequently sat on the opposite sides of the branches to the observer and occasionally peered around the branch. In this way they were obscured from view. When I moved around the tree the monkeys were visible in silhouette until they moved around the branch and out of sight. Other animals lay along the branches thus being invisible from below. This hiding was effective and a party of
monkeys could simply disappear from view. If I remained close for some time the animals moved slowly away through the trees and descended on the opposite side of the trunk to me, pausing to look before descending further and moving away over the ground.

When I approached the monkeys stealthily, concealing myself behind the vegetation, the monkeys soon became alert. Some would stand bipedally or ascend a tree and look around. This was sometimes accompanied by up, down and sideways movements (section 7.2.2). Barks were given and the group would move off over the ground. This is why it was inadvisable to hide while observing the animals. When I came upon the monkeys unexpectedly 5 - 20 m. away on the ground, or if I had been sitting quietly and a monkey had approached without realising that I was there, the monkey would pause for a moment flexing its limbs before running swiftly to the nearest trees. Flight was accompanied by repeated looking back towards the observer, sometimes with barking or (in infants) screaming. Hearing the call or seeing the swift movement, others fled. When I approached in the open to within 40 or 50 m. of the monkeys without being seen, the first animal to see me would stand and look or move away glancing behind. Even if it did not bark, its movements were usually seen by others which then looked towards me.

It was usually difficult to spot the first animal that barked. All age-sex classes except babies gave this call. The number of calls given by the first animal, and the extent to which others joined in, varied. Often only a single bark was given. A vigorous series of barks by several animals occurred when I continued to approach after the initial call, or when they were chased by predators (7.3.1). Bouts of vigorous barking by several animals included growls. Barking bouts were of variable duration. Adult males sometimes barked while watching the observer (7.2.2) and did this for up to 15 minutes, at a rate which settled down to 4 - 11 barks per minute. While those around them fed, they called and looked around between barks. Older juvenile males were also persistent callers, perhaps more so than adult males, but their calling usually followed flight and not vigilance behaviour. These juvenile males were mostly treed while calling; adult males
often called when on the ground. Persistent calling was also given in response to a concealed observer. (See also section 7.2.4).

7.2.2. Watching the observer: vigilance behaviour.

Monkeys looking at me often made a series of movements. These consisted of a bobbing movement, the head moving up, down and towards the observer, combined with sideways movements of the head and shoulders. The latter involved repeatedly putting the weight first on one hand and leaning towards that side (sometimes lifting the other hand) and then putting the weight on the other hand. A fully crouched position (either facing or sideways to the observer) and slight turns towards and away from the observer were also made. These movements were seen in three circumstances:

(1) When the path of vision between observer and monkey was partially blocked, the monkey used some of these movements to look over, under and around obstacles. These movements were seen in all ages of monkey and were also noticed when they were looking at, or for, other monkeys.

(2) The postures were also seen when there was a clear path of vision between the observer and the monkey. They were sometimes accompanied by repeated glances up into the branches (if sitting under a tree), paces to or from the observer, actual approach of the observer, raising the eyebrows, growling and pushing the head towards the observer, incomplete barking, yawning and flight. The animal appeared to be in a conflict between approaching, staying near, fleeing and attacking the observer and many of the components of these postures appeared to be intention movements. Up, down and sideways movements acted as signals; if the first monkey to spot me made them, others in the group would see the action and then look around towards me even if no bark had been given. The postures were easily produced by looking closely at an animal with binoculars; they stopped once the observer looked away.
Particularly intense and stereotyped behaviour was frequently seen in unhabituated animals. As the observer approached a group, or changed position, one or more adult males often moved into the open and sat 35 - 60 m. off. They frequently chose vantage points such as a tree stump or rock. This was occasionally preceded by walking or climbing towards or away from the observer or barking at him. The animal sat and watched the observer for periods of up to 15 minutes. During this time it engaged in few other activities, only occasionally would it scratch, autogroom, pick up a food item or look behind itself towards the rest of the group. Watching was sometimes accompanied by barking. Usually only the animals engaged in this behaviour were visible to the observer. At the start of a bout, or if stared at by the observer, the animal made the up, down and sideways movements described earlier. A simple experiment showed that these animals were keeping the observer under observation. When I moved so that the line of vision was broken they sometimes moved themselves until I was again visible. As I moved towards them a pace or so, they would move back usually keeping a distance of at least 40 m. between us. Some approaches by the observer were followed by barking. This behaviour was termed 'vigilance' behaviour. (It is a common tradition in N. Africa that each group has a 'guardian' responsible for keeping watch). Eventually the males got up, glanced at the observer, perhaps sat again briefly and then moved out of sight towards the rest of the group. Table 7.1 gives the number of times each individual in group 6 was seen to engage in this behaviour. Adult males were responsible for 74% of the instances and yet constituted only 12% of the group. Two of the three males were primarily responsible for this percentage. As the group became habituated (by other criteria) the frequency of vigilance behaviour also fell (section 7.2.4).

In the above cases the animals were definitely watching the observer; at other times this did not appear to be so. Adult and subadult males climbed high into a tree and sat looking around. This was sometimes preceded by the male moving out away from his group (Fig. 7.1); one of the few situations in which individuals left the main body of the group. Under these circumstances the males
FIGURE 7.1. Example of the movement of an adult male away from his group. From 1636\(\frac{1}{2}\) to 1648 the male sat in the open, high in a tree, and looked around.
<table>
<thead>
<tr>
<th>INDIVIDUAL</th>
<th>FREQUENCY OF VIGILANCE BEHAVIOUR</th>
</tr>
</thead>
<tbody>
<tr>
<td>AM1</td>
<td>8</td>
</tr>
<tr>
<td>AM2</td>
<td>1</td>
</tr>
<tr>
<td>AM3</td>
<td>9</td>
</tr>
<tr>
<td>Unidentified adult males</td>
<td>5</td>
</tr>
<tr>
<td>SM1</td>
<td>1</td>
</tr>
<tr>
<td>SM2</td>
<td>1</td>
</tr>
<tr>
<td>AF2</td>
<td>2</td>
</tr>
<tr>
<td>AF5</td>
<td>1</td>
</tr>
<tr>
<td>SF1</td>
<td>1</td>
</tr>
<tr>
<td>SF2</td>
<td>1</td>
</tr>
<tr>
<td>JF</td>
<td>1</td>
</tr>
<tr>
<td>All others</td>
<td>0</td>
</tr>
</tbody>
</table>

Based on the single group study.
rarely moved more than 100 m. from the nearest other animal. Some cases were related to the presence of other groups and were then sometimes accompanied by tree-shaking. In the cases now under discussion no other group was detected. This behaviour was particularly noticeable when the group was on the edge of the forest. Under such circumstances I was able to show that an animal facing in another direction responded to sounds, such as whistling and banging, by turning to face the source. As with vigilance behaviour, other age-sex classes were seen to do this but much less frequently. This may be thought of as 'look out' behaviour, in contrast to the vigilance behaviour that was directed at an already located, potential source of danger. After sitting and looking around for some minutes they would engage in other activities (e.g. autogrooming) or descend and join the rest of the group.

7.2.3. Protection of the young.

In response to barks, individuals ran to babies or babies ran to the nearest monkey and were carried. Babies were also carried when the monkeys were barking and growling at predators or when unhabituated monkeys had ascended the trees owing to the observer's presence. While approaching a group I sometimes inadvertently got too close to an infant or older baby on its own. Once this happened because the group had partially ascended the trees on my approach but the infant had not descended and moved off with the others. These infants gave vigorous screams and usually did not attempt to jump from one tree to another. Other monkeys looked towards the calling animal and gave barks or growls at the observer. In some cases one or more cautiously approached (repeatedly looking at the observer) and carried the baby or infant away. Only adult males and females were seen to collect babies and infants under these circumstances. This contrasted with cases where the baby called spontaneously and not because of my presence (section 11.4.1).
7.2.4. Responses of a habituated group.

The frequency of fleeing, vigorous barking, hiding and observer directed vigilance behaviour (Fig. 7.2) fell as I worked with each group. At the start of observations some groups were more scared than others and since I worked with numerous groups during the population study it was not possible to record the full process of habituation. When I started the single group study I had not worked with group 6 for three months. On first contact the group was quite scared but within two hours had settled down. After two days they moved within 40 m. of myself, while travel feeding, and within a week they were usually not even mildly disturbed by my presence. Vigilance behaviour was, however, seen for the first three weeks. Subsequently up, down and sideways movements were almost never seen and bipedal standing and looking at the observer was not followed by flight. During the population study several groups reached this stage almost as quickly and behaved normally at 30 - 40 m. In subsequent weeks I could regularly get to within 20 m. of the group 6 monkeys and occasionally as close as 3 m. For the reasons explained in section 1.4.2 I did not usually work this close.

When I approached the group in the morning, barks were given before I saw the monkeys. During the course of a day several bouts of barks were given at the observer. These were extremely short (e.g. chiefly one to four barks in a bout), separated from other barks by several minutes or hours and were either incomplete barks or a mixture of complete and incomplete calls. This indicated a relatively low level of arousal. They were chiefly given in response to my movements and as I left the group in the evening further barks were given. From June onwards I recorded, whenever possible, the identity of the monkeys that called at me (table 7.2). There was considerable variation between individuals within age-sex classes. Five monkeys (3 adult females and 2 subadult females) accounted for over 50% of the total bouts (57/105) given by identified monkeys. This data cannot be used to discover which animals were most likely to give the alarm in unhabituated groups; the animals that called frequently may have
FIGURE 7.2. The distribution of vigilance behaviour during the single group study. Vigilance behaviour occurred at the start of the single group study and when observations recommenced (arrows) after absence from the study area.
TABLE 7.2  THE FREQUENCY OF BARKING AND/OR GROWLING BOUTS AT THE OBSERVER BY GROUP 6 MONKEYS

<table>
<thead>
<tr>
<th>INDIVIDUAL</th>
<th>NUMBER OF BOUTS</th>
<th>INDIVIDUAL</th>
<th>NUMBER OF BOUTS</th>
</tr>
</thead>
<tbody>
<tr>
<td>AK1</td>
<td>6</td>
<td>AF6</td>
<td>4</td>
</tr>
<tr>
<td>AK2</td>
<td>0</td>
<td>SF1</td>
<td>8</td>
</tr>
<tr>
<td>AK3</td>
<td>4</td>
<td>SF2</td>
<td>5</td>
</tr>
<tr>
<td>SM1</td>
<td>4</td>
<td>SF3</td>
<td>13</td>
</tr>
<tr>
<td>SM2</td>
<td>2</td>
<td>JF1</td>
<td>0</td>
</tr>
<tr>
<td>JK1</td>
<td>4</td>
<td>JF2</td>
<td>3</td>
</tr>
<tr>
<td>JK2</td>
<td>3</td>
<td>JF3</td>
<td>4</td>
</tr>
<tr>
<td>JK3</td>
<td>0</td>
<td>IM1</td>
<td>0</td>
</tr>
<tr>
<td>AF1</td>
<td>2</td>
<td>IF1</td>
<td>1</td>
</tr>
<tr>
<td>AF2</td>
<td>9</td>
<td>IF2</td>
<td>2</td>
</tr>
<tr>
<td>AF3</td>
<td>18</td>
<td>BF1</td>
<td>0</td>
</tr>
<tr>
<td>AF4</td>
<td>4</td>
<td>IM2</td>
<td>0</td>
</tr>
<tr>
<td>AF5</td>
<td>9</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Based on identified individuals only, June 1969 to the end of the project.
adjusted less easily to the continuous presence of the observer. Other animals may have been just as alert to the presence of other stimuli. In spite of these calls the difference between group 6 and other groups was most noticeable. During intergroup encounters I had to be extremely careful not to influence the course of the encounter. While group 6 moved easily in my presence other groups were often quite scared and I had to remain at a distance.

Group 6 never ignored my presence entirely. If there was a sudden noise (caused for instance by a falling branch, a vigorous scream, or another group being attacked by predators) or if I made a sudden movement then they would start and glance up briefly. Young monkeys still called when I got too close. The monkeys were also more sensitive if they had just been disturbed by a dog or vehicle or if a mother had 'lost' her baby. On two occasions when females were looking for their babies (section 11-4-1), they started barking and growling vigorously at the observer who was moving and working in his usual way. This persistent calling made the whole group nervous and one female continued calling for 40 minutes after recovering her baby. Mothers with very young babies were sometimes slightly more scared of the observer than other individuals. Apart from this there was no indication that some monkeys were less likely to stay near the observer.

On three occasions several individuals (adult, subadult and juvenile males and adult females) approached me threateningly. They came through the trees and over the ground giving barks and vigorous growls. One incident was followed by vigilance behaviour and up, down and sideways movements were also made. On another occasion I had persistently been working close, taking photographs. Suddenly two adult males turned on me and rapidly advanced growling. I rapidly retreated as they came to within a metre of me and others joined in the calling. It took sometime for the group to settle down. This was the only time the monkeys attempted to attack a person or any other potential predator. Growls were occasionally directed at myself during agonistic sequences.

In spite of these isolated incidents the group was clearly habituated to my presence. For instance, at the end of the
As dogs almost invariably accompanied the flocks and herds it is important here to separate the monkeys' response to the dogs from those to the people and stock accompanying them. People on foot or horse back, without dogs, produced the same responses as those described for the observer with unhabituated groups. On hearing distant voices (e.g. 175 to 200 m. away) or the chopping of timber, the monkeys would pause and sit up looking towards the sound. They would then resume their activities or perhaps move slowly towards the trees if feeding in the open. Most people were indifferent to the monkeys, pausing only occasionally to look at them briefly before moving on. The occasional person threw stones at the monkeys or stood and shouted at them, but these were isolated incidents. There is no tradition of feeding monkeys in Morocco.

Vehicles using the Ain Kahla track and those collecting timber and charcoal deeper in the forest, disturbed the monkeys. With
people inside the vehicle the flight distance was reduced and the responses of the animals minimal. They partially ascended the trees, soon returning to the ground once the vehicle had passed. When feeding on the forest slopes they moved up to the trees if the vehicle passed 40-50 m. below them. Early in the study I sometimes watched the monkeys from a stationary vehicle when they were in the vicinity of a track. For unhabituated groups the reduced flight distance made it a useful hide.

7.3. RESPONSES TO PREDATORS.

This section is concerned with animal predators or potential predators. Panouse (1957) reported that the leopard (*Panthera pardus*) was at one time a predator of the monkeys. No panthers were recorded in the study area and they are extremely rare (if not extinct) in the Atlas. Some years previously a pair had been recorded at Ouiouane 16 km. from Ain Kahla. Man is probably the major predator of the monkeys (section 3.6); no other predator was known to be successful.

7.3.1. Jackals, dogs and foxes.

Lone jackals (*Canis aureus*) were seen to unsuccessfully hunt the monkeys on five occasions. When a jackal appeared near a group, vigorous barks were given on the side of the group nearest to the jackal. All the monkeys rapidly ascended the trees and the jackal rushed to and fro and stood beneath them looking up. The monkeys barked and growled vigorously at the jackal. All except babies called. While adult males sometimes climbed down onto low bushes and called just out of reach, most sat on higher side branches or climbed to nearer the top of the tree. Older babies and infants were carried dorsally during these sequences. One jackal harassed a group for at least seven minutes. Calling gradually died down in the five minutes after the jackal had left. On one occasion a similar response was given to a fox (*Vulpes vulpes*). In this case, however, they descended and fed while it stood facing the group only 40 m. away.
Most groups were chased at least once and sometimes several times a day by dogs from the herders' camps and those accompanying the flocks. This disturbance was reduced during the winter and spring when there was little grazing. The monkeys responded to these dogs in the way described for jackals and vigorous calling would often commence when the dogs were over 130 m. away. If the dogs were accompanied by people the monkeys ascended to the tops of the trees. When a group was widely spaced and under the trees, those furthest from the dog became alert but did not ascend the trees until the dog rushed towards them. Adult males were particularly prone to staying on the ground, repeatedly glancing at the dog before moving at the last moment. The loud choruses of calls could be heard at least 1 km. away. The monkeys of the group would look towards the calling and move under the trees (if they had been feeding in the open) or ascend them if the calling was particularly close. They did this without calling themselves. On some occasions the dogs were attracted to the group by calls given during agonistic behaviour. As with the jackals it took some time for the calling to cease and the monkeys sometimes did not descend to feed again until 15-30 minutes after the dogs had left. At other times they were, however, down and feeding within two minutes. Adult males were usually the first to descend and on some occasions they moved out towards where the dogs had gone and stood looking before they settled down to feed. The reasons for this variable time to descend remain unclear. There was possibly a tendency for the animals to remain treed if the disturbance occurred at a time when cessation of travel-feeding was expected. It was probably for the same reason that an increase in grooming sometimes followed such disturbances.

7.3.2. Birds of prey.

No bird of prey was seen to attack a monkey. The responses of the monkeys suggested that some species might be predators. Circling long-tailed buzzards (Buteo rufinus) produced little or no response. When they flew low over the group or settled near
them the monkeys looked up and growled vigorously. A similar response was given to small falcons (*Falco* sp) and to a large undetermined species of raptor (possibly *Circaetus gallicus*). Growls were given by most age-sex classes including infants and the initial call was followed by calls from other individuals. A few barks were also given.

7.3.3. Cautious approach to open ground.

It has been described how monkeys feeding on the bled or slopes of the forest soon returned to the trees at the slightest disturbance. In two circumstances the monkeys were observed to exercise particular caution before moving into the open.

In parts of the study area the monkeys had to cross the bleds to move from one part of the forest to another. Movement across one particular bled, that varied between 150 and 360 m. in width, was restricted to the narrowest points. At these places narrow spurs of high ground jutted out on each side from the forest. Growing on the forest end of these spurs were junipers and oaks. The monkeys descended slowly down the spurs feeding, moved swiftly across the open ground where the slightly elevated position gave a view over most of the bled and slowed down feeding again on the spur on the other side. When moving across open areas the adult males often sat in the open and fed while other animals ran by. If disturbed during a crossing they ran to the nearest trees and those left behind crossed only once the danger had passed. When group 6 crossed smaller open areas (e.g. 50 m. across), the group gathered and fed in the forest on one side, while several animals (usually adult males) sat in the open looking around without feeding.

When descending to drink in the open (from a rain water pool or at one of the wells) they moved with caution. A monkey would stop feeding, look about in an alert fashion and move towards the water, occasionally pausing and looking around. Having reached the water it would stand looking, drink and move back up towards the trees, perhaps pausing to look around as it did so.
7.4. RESPONSES TO OTHER ANIMALS.

Sheep, goats and cows. When these animals were unaccompanied by a herdsman or dogs the monkeys took little notice of them. They generally moved out of the way at 20-45 m., but occasionally stayed on the ground long enough for the sheep to be frightened by an adult male. They sometimes moved on hearing the sound of approaching sheep.

Wild pigs (Sus scrofa). Only one interaction between pigs and monkeys was seen. Grooming monkeys suddenly stopped and looked around. One stood bipedally looking through the trees. About 20 pigs then moved into the clearing and the monkeys all ran for the trees and ascended them. Upon seeing myself the pigs fled and the monkeys descended and fed. No barks or growls were given.

Birds. One or two ravens (Corvus corax) occasionally swooped down over the monkeys feeding in the open and settled amongst them to feed. As they flew in the whole group sometimes ran for the trees looking up as they did so. After a short while they would return and feed with the ravens. Infants and babies, sitting near watering points, would run away as pigeons (Columba palumbus) flew in to drink. On one occasion two starlings (Sturnus vulgaris) called loudly as they flew over the group. The monkeys looked up and then rushed briefly for the trees.

Other animals. Biting flies worried the monkeys as much as they did the observer; monkeys broke off from grooming or feeding to swat the flies that landed on or near them. On one occasion a carnivore (probably Genetta genetta) was seen 40 m. from the monkeys. There was no alarm.

7.5. RESPONSES TO OTHER STIMULI.

Flight responses could not always be attributed to the presence of potential predators. A monkey running through the group
or a vigorous scream during fighting was sometimes followed by the animals jumping up or running for the trees. The monkeys looked up and then moved slowly towards the trees as a small aeroplane flew overhead. They also responded to loud reports. For instance, when a sheet of ice cracked (as water melting upstream built up behind it) an infant leapt around looking towards the noise. The same response was seen when branches or snow fell from the trees. Animals also ran smartly out of the way of falling branches or rolling stones dislodged by monkeys feeding on the slopes above them. The above instances illustrate that while moving and feeding on the ground the monkeys were constantly alert. Monkeys turning stones or sitting feeding, sometimes gave vigorous startle responses leaping into the air with limbs splayed. The cause of this could not be determined.

7.6. DISCUSSION.

In this area predators were avoided by the monkeys remaining alert and running to the nearest tree if alarmed. If closely approached or chased by the predator they remained treed otherwise (and especially where people were involved) they moved off swiftly over the ground. The risk of being caught on the ground may be balanced by the need to keep up with the rest of the group, especially if the group was widely spread on disturbance and only some of the animals directly affected by the predator. In the Rif, Whiten (1972) saw monkeys dash for the nearest tree and ascend this only to jump to the ground and be chased again if the tree selected was an isolated one. This also suggests that keeping up with other individuals is important. Hiding may be an adaptation to man's hunting methods.

Since the main antipredator strategies were escape during the day and avoidance by sleeping in a safe place at night, provision for these activities will be key features in determining the distribution of the species. At Ain Kahla the animals used the cedars; near Ain Leuh and Azrou the oaks. At Ourika they escaped by running to the precipitous cliffs. In the Rif (Whiten,
personal communication) they probably sleep both in the trees and on cliffs. It is often argued that the multimale group is adaptive in habitats where predation is high, the emphasis being placed on potential confrontation between the males and the predator (Crook and Gartlan, 1966; Denham, 1971; Eisenberg et al, 1972). These arguments are usually based on open country species and no mechanism has been suggested to satisfactorily explain the value of multimale groups in forest floor primates. Where predators may creep up stealthily and undercover on terrestrial animals, there will be safety in numbers since an individual may gain from the wariness of others. Most individuals (except babies and perhaps actively playing infants and juveniles) are probably equally good at detecting a predator's approach and since escape, and not defense, is the main antipredator strategy, a multimale group does not seem to be at an advantage.

It is important, however, to consider the function of vigilance behaviour. Whiten (1972) also saw this in the Rif. This behaviour suggests that under some circumstances the best response to a potential predator may be to keep it under observation. An actively breeding adult male will probably have several young in the group and vigilance behaviour may be a good way of protecting them. Since it is unlikely that males recognize their own offspring, each male will probably benefit from the behaviour of its fellows. This suggests a reason for the maintenance of multimale groups in this habitat. Why should this behaviour be chiefly restricted to adult males? In a natural state without shooting, staying in the open (and especially upon the ground) may involve a risk for the vigilant animal. This risk may be too high for females suckling young, and the potential genetic gains may not balance the potential losses (Hamilton, 1963) for subadult males and other non adults that have siblings but not young of their own. It is interesting in this context, that it was only mothers and adult males who rescued babies and infants when these had been isolated by the observer.

No one factor can be used to explain the presence of multimale groups in this species. This type of group is common to all mangabeyes, macaques and baboons * living under a wide variety of conditions. We do not know when this group structure first

* It is modified in Papi hamadryas.
developed and for what conditions it was adaptive. The whole social behaviour of the animals revolves around this group structure and the need for conformity may be a constraint against change (Crook, 1970). Known changes in predation pressure and the distribution of food may be required to produce any major change in group composition and structure (other than group size).

7.7. SUMMARY.

A variety of responses to people and predators (jackals, dogs, foxes and possibly birds of prey) are described. The sighting of a person or mammalian predator was followed by barking and flight to the nearest trees. If approached or chased they ascended or remained treed; otherwise they descended and moved away on the ground. Flight distance varied unpredictably from 6 - 200 m. They were constantly alert while feeding and 'false alarms' were frequently produced by other stimuli. Additional responses to persons included hiding behind branches and up, down and sideways movements of the head and anterior parts of the body. These movements were used to look around obstacles; while looking at the observer with a clear path of vision and during vigilance behaviour. In the latter two cases the animals appeared to be in a state of motivational conflict. Vigilance behaviour involved moving into a prominent position and sitting and watching the potential predator. It was performed chiefly by adult males, who also engaged 'look out' behaviour (not directed at a specific object), and were the least nervous animals in potentially dangerous situations. Infants and babies were carried during encounters with predators and when they were isolated from the rest of the group they were rescued by adult females and adult males. Special caution was adopted while crossing open ground.

The group studied in detail became habituated to the observer while not changing its responses to other persons. During the course of habituation the frequency of fleeing, vigorous barking, hiding, observer directed vigilance behaviour and up, down and sideways movements fell. Low intensity barks were still however given, chiefly by adult and subadult females.
These forest floor primates did not confront predators but escaped from them by ascending the trees. Since most age-sex classes could detect a predator's approach, a multimale group living in forest does not seem to be at an advantage. It is suggested that life in a multimale group may be an advantage to reproductive males, since several males may be available for the potentially dangerous activity of vigilance behaviour and thereby (indirectly) protect each other's young.
8. BEHAVIOUR REPERTOIRE

Macaca sylvanus has a rich and varied behaviour repertoire showing many similarities with other macaques * and other Cercopithecinae. Since there is no catalogue of behaviour patterns available for this species and in order to permit comparison with other macaques, I have described the repertoire in some detail. The emphasis is on describing the behaviour patterns and, where appropriate, the context, associated behaviour and response of other individuals. The dynamics of interaction between individuals (comprised and mediated by these behaviour patterns) is analysed in subsequent chapters.

8.1. DEFINING UNITS OF BEHAVIOUR.

Descriptions and catalogues of behaviour patterns are cumbersome but essential, since behaviour patterns are the raw material of the ethological method (Tinbergen, 1951, Bateson, 1968). The behaviour patterns presented here are motor patterns or what Hinde (1970) has termed "spatio-temporal patterns of muscular contraction". They include, to a lesser extent, some descriptions "in terms of the consequences of behaviour". Ethograms are almost always heterogeneous in the level of description used; nevertheless the patterns are usually recognizable by other observers (Beverstein, 1970). It is first necessary to discuss the criteria on which the catalogue is based. The following was partly stimulated by the comments made by Altmann (1968).

* For the behaviour patterns of other macaques see the following:

(1) Patterns were isolated from the continuous flow of behaviour by, to quote Altmann (1965), attempting to divide "the continuum of action wherever the animals do". If the resulting units of behaviour "affect the behaviour of other members of the social group, then they are social messages" (see section 8.2.1). This approach places emphasis on the physical structure of the behaviour pattern and its communicative capacity without implying that each pattern has one function. Stridhaker (1967, p. 319) considered that a repertoire should be based on "both the natural units of behaviour and upon the communicatory function of the behaviour patterns as manifested by the response(s) which they evoke in other animals". Responses may, however, vary so much with context that I have (with a few exceptions) defined patterns in terms of their structure and only then given details of context and responses. Mixed catalogues (based on both the structure and functions of patterns) may hinder comparisons between species (Gautier-Hion, 1971).

(2) I have pointed out when patterns were particularly rare but in general, behaviour patterns are included irrespective of their relative frequency. Items are described with variable precision and caution is therefore required when comparing the repertoire size of different species. Further study may well add new patterns and refine those included. Since, except during the initial phase of the project, there was only one observer there could be no interobserver reliability tests. It is expected, however, that other observers should have no difficulty in recognizing the patterns defined. Inter-observer reliability tests should be treated with caution; a high correlation between observers may simply mean that they have reached agreement on where to interrupt the flow of behaviour and may say little about why the 'cut' was made where it was. This will be particularly true where continuous and not discrete patterns of behaviour are involved.

(3) Unless indicated to the contrary, the patterns listed are 'discrete' (in the sense of Hockett 1960, quoted by Altmann, 1967). Continuous patterns are split into smaller units at the point where these units appeared to be most physically distinct from each other and are listed together. Continuous patterns...
(e.g. the series lip-smacking face — teeth-chatter face — silent bared-teeth face with head flagging) often represented changes in intensity of a signal or response. With more information many of the discrete units might be classified as part of a continuous system. Most calls were part of a continuous system and with them problems of analysis were particularly acute.

(4) Patterns are divided into those which are communicative (with direct social significance) and those which were not. Some of the latter (e.g. drinking and feeding) did convey information to other individuals but this was of a different sort to that carried by the communicative patterns.

(5) Patterns are generally physically distinct in the sense that an act was either one pattern or another; it couldn't be both. (This criteria is violated in a few instances).

(6) Patterns could occur at the same time e.g. 'sexual presentation' and 'look at'. Such combinations are not themselves considered as separate patterns. Some combinations are however physically impossible e.g. 'face to object's anogenital area' and 'move towards'. When two patterns appeared in combination this did not mean that they started and finished simultaneously. Two patterns which always occurred simultaneously would be recorded as one pattern and not two.

Altmann (1962, 1965) attempted to "obtain a complete catalogue of mutually exclusive socially significant behaviour patterns". "Such that one, and only one, of them must occur at each trial in every social interaction". While highly desirable for stochastics this aim is clearly unobtainable. Patterns last for variable lengths of time and must in some cases overlap. e.g. Altmann's 'presents to' must often coincide with 'looks at'. With a detailed catalogue an animal would only rarely be performing one pattern.

(7) Patterns are described in terms of the monkey who made the action and not the monkey who received it.
(8) Some patterns were brief (e.g. look at) while others were more lengthy (e.g. grooming). No account is taken of this in their inclusion in the catalogue.

(9) Constellations of behaviour patterns such as 'mounting' have been split up into their discrete component patterns. The extent to which these patterns were put together often represented differences of intensity.

8.2. PHYSICALLY DISTINCT PATTERNS OF BEHAVIOUR WHICH ARE THOUGHT TO BE COMMUNICATIVE.

8.2.1. Introduction.

These patterns are thought to be communicative in the sense that they probably directly influenced the behaviour of other individuals. Evidence that this may be so will be found in subsequent sections but it was not my aim to analyse in depth the sequence of patterns used in communication. My aim was to describe the major components of behaviour and to analyse the behaviour within a group, chiefly in terms of the frequency with which these patterns (or constellations of them) were used between individuals. Where recording techniques have probably not unduly biased the data the distribution of the patterns (or constellations of them) is given in subsequent chapters. It would be pedantic to insist that all motor patterns should be tested empirically to discover their meaning before any analysis based on them was carried out. Such an approach would ignore the considerable qualitative evidence (and the more limited quantitative evidence) of their importance in the communication of macaques and other primates. It would also assume that the techniques available for such an analysis (e.g. a stochastic approach based on Markov chains (Altmann, 1965)) are satisfactory in their application and interpretation. For instance, most Markov analyses of inter-individual transitions of behaviour assume that intra-individual transitions do not confound the analysis. If any inter-individual transition is found to occur significantly more than
chance then it is ascribed to the patterns having a communicatory function between animals. The reverse applies when intra-individual transitions are examined in a social situation (Slater and Ollason, 1972). Many studies ignore the context of the signalling and assume that interaction within a group is based on dyads. This is often the case but there will be many instances in which the presence or absence of a third individual modifies the behaviour of dyads. To facilitate interpretation authors often remove the 'noise' from the system by omitting the rarer transitions. It is easy to think of cases of relatively rare behaviour patterns which are nevertheless extremely important. Some transitions between behaviour patterns are used in subsequent chapters; the techniques used and their limitations are discussed in section 9.3. They provide evidence for the communicative function of some of the patterns discussed here.

It is useful to include in any behaviour repertoire a description of the behavioural context(s) (stimulus situations, types of interaction) in which each pattern was observed. Context may be defined in terms of the underlying motivation or with respect to the characteristics of the social interactions in which the pattern occurred. Some patterns clearly do indicate the motivational state of the animal giving the gesture but, as with investigating the communicatory function of motor patterns, special techniques of data collection and analysis are required before behaviour sequences can be used to indicate underlying 'motivational systems'. In the following, context is chiefly defined in the second sense by giving typical examples of the interactions in which the pattern was seen. These examples are not intended to be exhaustive. I have intentionally not defined context in terms of a formal list of 'stimulus situations' (Struhsaker, 1967b). Many social interactions included several different types of behaviour (e.g. maternal and agonistic) and behaviour patterns occurring in such interactions could legitimately be classified as occurring in any of these. There is also a danger of circularity; the patterns themselves contribute to the behaviour that enables one to classify an interaction as including, for instance, agonistic or sexual behaviour. In the following I have therefore placed the emphasis upon how the patterns were
used in different types of interaction. Notes on the responses of the monkey receiving the behaviour pattern are also given. Again these are not intended to be exhaustive and generally only examples of the most frequent responses are listed.

To be concise I will use 'subject' to describe the animal performing the behaviour and 'object' to describe the animal to which this behaviour was directed or the animal which appeared to respond. Each pattern is listed under the headings of description (D), context (C) and response (R). Where responses varied with context and with variations in the structure of patterns the corresponding sections are linked using Roman numerals. Almost all age-sex classes were, at one time or another, seen to give most patterns. Patterns are listed in table 8.1 and some are illustrated in the plates in this and other chapters.

8.2.2. Movement of one animal relative to another.

These patterns resulted in a change of distance between individuals. Most were accompanied by other patterns.

(1) Move to.

D. Subject approached object by any of the patterns of locomotion. Accompanied by a variety of facial expressions. When associated with flight of the object and the approach continued this was scored as chase.

C. Almost every context.

R. Responses included move away from, present, ignore, look at, most expressions, cradle and many others.

(2) Move from.

D. Converse of (1).

C. Almost every context. Frequently the last behaviour pattern in a social interaction. During agonistic behaviour this was usually accompanied by the staring bared-teeth scream face, the teeth-chatter face or the lip-smack face.

R. Frequently no response. Responses included move to, follow, look at, staring open-mouthed pout-face, teeth-chatter face.
TABLE 2.1. PHYSICALLY DISTINCT BEHAVIOUR PATTERNS WHICH ARE
THOUGHT TO BE COMMUNICATIVE

Movement of one animal relative to another.

1. Move to
2. Move from
3. Move near
4. Intention movement away from
5. Turn away from (avoid)
6. Wait for
7. Follow

See also 89, 90.

The orientation of one animal to another.

8. Sit by side
9. Sit sideways
10. Sit facing
11. Stand by side or behind
12. Stand sideways
13. Stand facing
14. Lay down infront
15. Sit in lap
16. Sit behind

See also 17.

Sexual behaviour.

17. Present
18. Head bob/head duck
19. Face to object's ano-genital area
20. Hand to object's ano-genital area
21. Push on shoulder or side
22. Hands on waist
23. Grip hind legs
24. Pelvic thrusts
25. Mountee reaches back
26. Mountee grips hind leg of mounter

See also 6, 7, 16, 75, 76, 85.

Maternal behaviour and other interactions involving babies and infants.

27. Dorsal embrace gesture
28. Cling to dorsal surface
29. Cling incompletely to dorsal surface
30. Sit or stand on
31. Prevent clinging to dorsal surface
32. Ventral embrace gesture
33. Hold to ventrum
34. Cling to ventral surface
35. Cling incompletely to ventral surface
36. Cradle
37. On nipple
38. Manipulate nipple with fingers
39. Prevent suckling or manipulation of nipples
40. Restrain
41. Shake
42. Touch, grab, pull, push, hold
43. Lift
44. Pull by thighs (behind-lifting)
45. Pull by arms

See also 5, 7, 58, 59, 72, 75, 76, 77, 78, 79, 82, 83, 84, 86, 87, 88.

Other non-agonistic behaviour.

46. Allogrooming
47. Solicitation for allogrooming
48. Ventral-ventral embrace (hugging)
49. Ventral-dorsal embrace
50. Arm under belly/arm over back
51. Arm around back, shoulders or waist
52. In contact
53. Face to head
54. Head-flagging
55. Ignore
56. Look at
57. Look from
58. Look for (search)
59. Play
60. Hand to own ano-genital area
61. Tree-shaking

See also 42, 75, 76, 77, 79.

Agnostic behaviour.

62. Look apprehensively towards
63. Stand rigidly
64. Lunge
65. Crouch
66. Attack
67. Bend face towards back

See also 4, 17, 22, 23, 24, 25, 26, 48, 50, 56, 57, 70, 71, 72, 73, 74, 75, 76, 81, 82, 83, 84.

Expressions.

68. Relaxed face
69. Alert face
70. Tense-mouthed face (stare)
71. Staring open-mouthed face
72. Staring open-mouthed pout face
73. Staring open-mouthed pant face
74. Staring bared-teeth scream face
75. Lip-smacking face
76. Teeth-chatter face
77. Silent bared-teeth face
78. Bared teeth-gecker face
79. Relaxed open-mouthed face

Calls.

80. Barks
81. Growls
82. Screams
83. Chups and cheeps
84. Chatters
85. Jabbers
86. Geckers
87. Squeaks
88. Purr
89. Grunts
90. Clear calls
(3) **Move near.**

D. Subject locomoted near the object but without approaching it directly. Usually not accompanied by any specific facial expression.

C. Seen during travel-feeding when one monkey moved near another (and sometimes sat near it) without approaching it directly (responses (i) and (ii)) or during periods of non-agonistic behaviour (responses (i) and (iii)).

R. (i) Look at, ignore, teeth-chatter, (ii) look apprehensively, intention movement away from, move from, staring open-mouthed pout face, tense-mouthed face, move to, staring open-mouthed face. (ii) Move to, solicit allogrooming.

(4) **Intention movement away from.**

D. Standing or sitting subject leant away from object sometimes lifting a forelimb from the ground or standing if previously seated. Usually accompanied by look at, look apprehensively at or look from.

C. A variety of situations during which a monkey did one of the following to the subject: move to, move near, look at, tense-mouthed face, staring open-mouthed face, staring open-mouthed pout face. Also seen in situations when one might judge from the flexing of the object's body that a threat was imminent. Frequent situations included a higher ranking animal sitting near or looking at the subject, or a mother looking towards a juvenile or subadult female who was touching her baby.

R. Ignore, staring open-mouthed pout face, look at, staring open-mouthed face, tense-mouthed face, lip-smack face, teeth-chatter face, move to.

(5) **Turn away from; avoid.**

D. Subject turned its back on and sometimes moved away from the object. This was not accompanied by any of the typical signs of fear e.g. look apprehensively towards and the staring bared-teeth scream face. See addendum p 272.
C. Monkeys seated cradling a baby sometimes avoided others as they approached and attempted to look at or touch the baby. It frequently terminated such interactions.

R. Follow, look at, move to.

(6) Wait for.

D. (i) Subject waited until object had finished an action which it then performed. (ii) Subject moving away from object paused (usually looking at the object) while the latter moved towards or near it. Once the object was closer the subject moved away from the object and may be waited again.

C. (i) Seen at drinking and feeding positions. (ii) Seen in consort pairs, the female frequently waiting for the male and thus being (in the immediate sense at least) responsible for keeping the pair together.

R. (ii) Move to; move near; ignore.

(7) Follow.

D. Subject kept close behind object or moved along some distance behind it (usually along the same route) with its behaviour clearly orientated towards the object. (This differed from chase in which the leading monkey was escaping).

C. Babies and infants frequently followed their mother or another animal (responses (i) and (iv)); monkeys followed others that carried babies and infants; mothers followed others that carried their babies (responses (ii) and (iv)); consorting monkeys followed each other (response (iii)).

R. (i) Dorsal or ventral embrace, pull. (ii) Tense-mouthed face, staring open-mouthed pout face. (iii) Sexual behaviour. (iv) Wait for, move to.
8.2.3. The orientation of one animal to another.

These patterns followed the approach of the subject to another and preceded more complex and, in many cases, non-agonistic behaviour. There was a continuous series of orientation postures but it was convenient to single out those described below. Most of the patterns were un stereotyped; presentation and the patterns used to solicit grooming were exceptions and were major social signals (they are described in later sections). The remaining patterns often did not produce a noticeable response from the object, but probably served nevertheless to position the subject for further interaction and so indicated its mood and intentions to the object.

(8) Sit by side.

D. Subject sat by side of object either in contact or within touching distance.

C. Many non-agonistic situations e.g. a baby or infant sitting near its mother; monkeys sitting by others in possession of a baby and vice versa; subject approached a resting monkey and sat near it.

R. Look at, ignore, avoid, solicit allogrooming, allogroom, pull, teeth-chatter face.

(9) Sit sideways.

D. Subject sat with its side towards the object, either directly in front of it or to one side. The distance between them varied with the subject sometimes sitting more or less in the object's lap or out of reach. The object was usually, but not always, seated. (An intermediate between this and stand sideways was crouching sideways to the object).

C. Males carrying babies dorsally to other males often took up this position.

R. Look at; touch or mouth the baby or infant on the subject's back; ignore, teeth-chatter face.
(10) **Sit facing.**

D. Subject sat facing and within touching distance of the object. (Excluded ventral – ventral embrace).

C. Frequently seen in interactions involving babies and infants. e.g. subject carrying one on its back sat facing the object; subject with baby to its chest or in its lap sat facing the object; or in equivalent situations when subject without a baby approach an object and sat facing it before initiating play. A version of this posture was used to solicit allogrooming.

R. Look at, solicit allogrooming, allogroom, touch or pull baby carried by subject, staring open-mouthed pout face, tense-mouthed face, teeth-chatter face.

(11) **Stand by side or behind.**

D. Subject stood by side of or behind the object either in contact or within touching distance. Usually accompanied by looking at the object.

C. Typically seen when subject approached an object seated with a baby or infant (response (i)) or when a male approached a female as part of a sexual sequence (response (ii)).

R. (i) Look at, move away from, avoid, staring open-mouthed pout face, tense-mouthed face, ignore; (ii) present, look at.

(12) **Stand sideways.**

D. Subject stood with its side towards the object either directly infront of it or to one side. The distance between them varied from in contact to out of arms reach. In contrast to presentation, the subject's behind was not noticeably directed at the object. Usually accompanied by looking at the object.

C. Sometimes seen when a monkey (not a mother) carrying a baby or infant approached another.

R. Look at, ignore, staring open-mouthed pout face, tense-mouthed face, pull or touch the baby carried by the subject.
(13) **Stand facing.**

D. Subject stood facing the object. The distance between them varied considerably.

C. (i) Often followed or accompanied the subject receiving or giving threatening gestures. For instance, after fleeing a monkey would frequently turn and face the object screaming and giving the staring bared-teeth face. (ii) Preceding non-agonistic interaction, such as when a subject carrying a baby or infant approached the object or vice versa. Monkeys approaching in this fashion were, however, sometimes threatened.

R. Look at, ignore, move to, staring open-mouthed pout face, tense-mouthed face, teeth-chatter face.

(14) **Lay down infront.**

D. Subject lay down (on one side with legs outstretched or on ventrum with legs drawn under the body) in front of and within arms reach of the object.

C. One of the patterns used to solicit allogrooming.

R. See behaviour pattern No. 47.

(15) **Sit in lap.**

D. Subject sat in the lap of the object looking away from the latter. They were in dorso-ventral contact.

C. Frequently followed an approach by a subject carrying a baby or infant (usually dorsally) to a seated object. Often preceded by standing sideways or presenting. Sometimes accompanied by the subject handling the object's genitalia.

R. Ventral-dorsal embrace; teeth chatter face, bend face towards back (with or without mouthing fur), touch, pull or mouth the baby on the subject's back.

(16) **Sit behind.**

D. Subject sat behind a seated, presenting or otherwise standing monkey. With a seated object they were therefore in a dorso-ventral position.
C. (i) During seated mountings when subject sat behind a standing or presenting object. (ii) When subject sat behind a female and examined her ano-genital area. (iii) When a subject sat behind a monkey carrying a baby or infant on its back. In this case it was frequently followed by ventral-dorsal embrace.

R. In most cases the object monkey maintained its position and the subject made the next move. Sometimes, for instance during inspections of a female's anogenital area, the object moved from the subject.

8.2.4. Sexual behaviour.

Sexual behaviour is defined (section *) as courtship, copulation and masturbation. In addition to occurring during sexual behaviour many of the following patterns were incorporated into 'genital displays'. These were important components of agonistic behaviour and the behaviour between babies, infants and older animals, both between and within the sexes. Where it is important to distinguish between the use of a pattern in sexual and non-sexual situations, the patterns are qualified accordingly. (See plates 8.1 and 8.2)

(17) Present.

D. The subject stood stiffly (either in front of or to the side of the object) and with its behind turned towards the object. Often accompanied by looking at the object and sometimes by backing up towards it.

C. (i) Posture used by a female to solicit copulation following an approach to a male. Females also presented if approached by males. Usually followed by the male inspecting the female's genitalia and mounting.

Examples of the use of this pattern in non-sexual situations included: (ii) Following an approach by the subject to a social interaction (e.g. a mother and baby, males and baby). Here presenting was seen with or without the subject receiving a threat and was often accompanied by the teeth-chatter face. (iii) Given in response to a *Appendix A.
PLATE 8.1. SEXUAL BEHAVIOUR

(a) A subadult male sits behind a swollen adult female and touches and looks at her swelling. (SM1, AF3, group 6).

(b) An adult male starts to mount an adult female by placing his hands on her waist.

(c) An adult female runs from an adult male in response to him touching her swelling. (AM1, AF1, group 6).
PLATE 8.2. SEXUAL BEHAVIOUR SEQUENCE

A series showing part of a consort sequence between an adult male and adult female. The sequence starts (0 mins.) with the female approaching and presenting. He examines her genitalia and (at 4 mins.) they copulate. He leaves and she follows. At 22 mins. she presents and starts to groom him. She presents again (25 mins.) and he grooms her (a). She presents at 37 mins., he inspects her (b), she grooms him (c and d) and later they rest in contact (e). At 40 mins. he turns, she presents (f), he copulates with ejaculation (g); she reaches back and jabbers. On dismounting they rest in contact (h). Subsequently she grooms him briefly several times, presents again, is ignored and leaves him at 53 mins. He follows and they rejoin the group and move independently 74 mins. after the sequence started.
A series showing part of a consort sequence between an adult male and adult female. The sequence starts (0 mins.) with the female approaching and presenting. He examines her genitalia and (at 4 mins.) they copulate. He leaves and she follows. At 22 mins. she presents and starts to groom him. She presents again (25 mins.) and he grooms her (a). She presents at 37 mins., he inspects her (b), she grooms him (c and d) and later they rest in contact (e). At 40 mins. he turns, she presents (f), he copulates with ejaculation (g); she reaches back and jabbers. On dismounting they rest in contact (h). Subsequently she grooms him briefly several times, presents again, is ignored and leaves him at 53 mins. He follows and they rejoin the group and move independently 74 mins. after the sequence started.
PLATE 8.3. ALLOGROOMING

A subadult male grooms an adult female. She leans forwards to facilitate the grooming of the back of her head. (SM1, AF6, group 6).
threat, chase or to the object moving to or near the subject without threatening it. (iv) The subject, having been involved in an agonistic interaction with another, approached the object (often not involved in the interaction) and presented. Such sequences were frequently followed by the presenter grooming the object and/or they developed into protected threat sequences. (v) Following the subject threatening the object, the subject sometimes presented to the latter which mounted it. (vi) Subject carrying a baby dorsally, approached object and presented.

R. Ignore, move from, move to, sit behind, stand by side, or behind, place face to anogenital area, touch anogenital area with hand, mounting sequences, allogrooming, look at.

Presentation by younger animals (infants and juveniles) was often followed by a seated mounting. In this the subject sat behind the object, placed its hands on the latter's waist, bent its face down to its back and sometimes mouthed the fur on its back. This was seen in most circumstances where non-sexual mountings were expected and seemed to be chiefly related to the relative size of the participants. Females as well as males assumed the mounter's role.

(18) Head bob/head duck.

D. Subject half presenting to object, or more or less facing it, looked at it and bobbed its head up and down. (Excluded up, down and sideways movements).

C. A rarely seen posture that sometimes was given by a female to her consort, apparently instead of a presentation.

R. -

(19) Face to object's ano-genital area.

D. Subject placed face towards the ano-genital area of a standing or sitting monkey or sat in front of it and bent down into its groin.

C. (i) A frequent component of courtship. Given by the male to the female after an approach by either partner or presentation by the female. The male typically placed his nose close to the genitalia or remained some way off and looked at her behind. In the former situation it was often preceded or accompanied by the male placing his
hands on the female's rump. Presumably both visual and olfactory stimuli were examined; within the space of a few minutes males sometimes made a close examination of both swollen and non-swollen females. Females and young animals occasionally examined swellings. (ii) This pattern invariably accompanied the behind-lifting of babies and infants. The subject usually teeth-chattered (or less frequently lip-smacked) at the object's behind. Under these circumstances they did not usually appear to be simply examining visual and olfactory stimuli. (iii) Also seen in response to presentation in many of the non-courtship situations listed earlier. (iv) In response to a sitting or standing monkey outwith any of the above situations e.g. during play and by infants and juveniles who did this to each other or to a baby or infant that was suckling. (v) When males were sitting facing each other and interacting over a baby, one male (invariably the subordinate) occasionally bent its face down to the other's groin.

(20) Hand to object's ano-genital area.
D. Subject touched or manipulated object's ano-genital area.
C. (i) Frequently accompanied face to object's ano-genital area. For instance a male sitting behind a female often placed his hands on either side of her swelling or to her genitalia and then brought his face close. A standing male often raised one hand to the ano-genital area while looking at this. (ii) Accompanied reaching back by a mountee during mounting. (iii) During interactions between males and babies one male (invariably the subordinate) placed its hand into the other's groin. (iv) Subadult and juvenile females manipulated the penis of an infant or baby while sitting with him and his mother, or between bouts of play.
R. Present, move from, look at, groom, stand still.

(21) Push on shoulder or side.
D. Subject (male) approached a seated female and pushed it with one hand or gripped the fur on the female's back and pulled her to her feet.
C. Pattern used by a male to get a swollen female to stand, usually followed by examination of her ano-genital area.
R. Ignore, lean to one side and slightly lift the behind, stand up, look at, present.

(22) Hands on waist.
D. Subject, standing or sitting behind standing object, placed its hands on either side of the object's body.

C. Important component of mounting and it was usually followed by the subject gripping the hind legs of the object. Incomplete mounts were recorded when the latter did not occur. Seen also in seated mountings.
R. Stand still, present, look at, move from.

(23) Grip hind legs.
D. As the subject climbed onto the object's back to assume the copulation position it gripped the object behind the knee first with one foot and then the other. The subject was then said to be mounted upon the object.

C. Seen in all except seated mountings. (i) It occurred therefore in all the situations listed under 'present'. Mounts between males and females thought to be accompanied by intromission were recorded as copulation. Some mounts were achieved without gripping the hind legs of the partner; infants, for instance when mounting adult animals, almost assumed the dorsal carriage position. (ii) Occasionally mounting was not preceded by presentation. One male sometimes ran to and mounted another while the latter was not presenting. Seated animals were occasionally mounted. Mounting was accompanied by pelvic thrusts, bending the face towards the back of the partner and mouthing its fur, lip-smack and teeth-chatter faces.
R. Stand still, move from, look at, teeth-chatter.

(24) Pelvic thrusts.
D. Subject mounted on object gave rhythmic dorso-ventral movements of the pelvis. Some copulations were accompanied by ejaculation.

* I refer to these as 'complete mounts' when it is necessary to specifically distinguish them from 'seated mounts' (p.160).
C. During all except seated mountings.

R. Look at, teeth-chatter face, move from, mountee reaches back, jabber call.

(25) Mountee reaches back.

D. While mounted by another animal, the subject reached around towards the mounter's hind leg or towards its own ano-genital area or that of the mounter. The hand passed either outside or inside the thigh and the subject's head was bent around towards the object.

C. All mounting situations including seated mountings. With complete mountings it was usually only given once pelvic thrusts had started.

R. Look at, teeth-chatter face, mounting continues.

(26) Mountee grips hind leg of mounter.

D. Subject being mounted reached around and gripped the mounter's leg at the level of the knee or lower leg. Subject's head was bent towards the object. With seated mountings the subject occasionally gripped the mounter on the arm.

C. Seen particularly during copulations but also in other mounts. Often followed 'mountee reaches back' and was accompanied by the teeth-chatter face.

R. Look at, dismount, mounting continues.

8.2.5. Maternal behaviour and other interactions involving babies and infants.

Most of these patterns were important components of maternal care and were also used during female and male care sequences. Some patterns (e.g. pull by thighs, pull by arms, shake) were not components of maternal care and were directed at babies and infants by older animals.
(27) **Dorsal embrace gesture.**

A complex of postures that are grouped together because they were all followed by the object approaching the subject and climbing onto its back. Variations included: (i) Subject stood with its behind towards the object and looked at it over its shoulder. (ii) As (i) but accompanied by the subject teeth-chattering (sometimes lip-smacking) and slightly lowering its rear or backing towards the object. (iii) Subject crouched completely and looked over its shoulder at the object and teeth-chattered. (iv) Seated subject went into a crouched position as (iii). (v) Standing subject touched the object. (vi) Subject pushed or pulled the object onto its back.

C. Given only to babies or infants to induce them to cling dorsally. (i) - (ii) - (iii) - (vi) can be considered as a series showing increased intensity. If posture (i) failed then a subject frequently tried (ii) and so on. (vi) was also seen when an object that was being carried started to slip off the subject's back.

R. Move to, cling dorsally, ignore.

(28) **Cling to dorsal surface.**

D. Subject clung to the object's dorsal surface. When the object was standing then the subject held on well forwards lying over the object's shoulders and chest and gripped its fur with its hands and feet. The head was held to one side, the face looking over one of the object's shoulders. As the object sat, or if the subject clung to a monkey already sitting, then the subject often slid down its back and rested its feet on the ground, still keeping a hold of its fur with the fingers. As the object stood, the subject pulled itself forwards into the position described above.

C. Babies and infants clung to the dorsal surface of other animals in a variety of situations described elsewhere. When the object stood or moved with the subject clinging in this or any of the other ways subsequently described, then this was recorded as the subject being carried. Babies clinging dorsally sometimes gave the purr call. (Excluded ventral-dorsal embrace).
R. Carry, stand or sit with subject on back, prevent dorsal clinging, teeth-chatter and lip-smack faces, look at.

(29) Cling incompletely to dorsal surface.

D. Subject clung to object in one of several variations of the posture just described. (i) Subject held on over the rump or middle-back, head facing the object's anterior or posterior. (ii) Subject sat on the object's rump 'jockey style'. (iii) Subject clung onto the fur on the object's limbs and hung down these, either the correct way up or upside down.

C. Seen chiefly in young babies that had just started to cling dorsally.

R. Object ignored this and kept carrying the subject; object stopped moving and pushed the subject onto its back or pulled it to its ventrum; prevent clinging to the dorsal surface.

(30) Sit or stand on.

D. Subject sat or stood on the shoulders, back, head or side of the object or climbed over it.

C. Seen when babies and infants climbed over their mothers and other animals.

R. Ignore, look at, pull, teeth-chatter and lip-smack faces.

(31) Prevent clinging to dorsal surface.

D. Subject prevented the object from clinging to it by turning towards it and pulling it from its body, by rolling over or by shaking itself.

C. Compared with the numerous occasions on which babies and infants were carried this was rarely seen. Occurred sometimes immediately after the start of dorsal clinging, or if an infant or older baby clinging to its mother's back had persistently (and inspite of numerous attempts to stop it) tried to reach over her shoulder to the nipple.
R. Object ceased to cling dorsally, move from, scream.

(32) Ventral embrace gesture.

D. Subject cupped its hand around the object's back and pulled it, ventrum first, towards its own ventrum.

C. A brief gesture used by a monkey carrying or sitting with a baby to induce it to cling ventrally. Seen when the subject moved, got up, changed from walking to running, jumped or if the baby relaxed its grip while being carried. If the baby was sitting some way away this action was preceded by a sweeping action with the hand or the baby might be partially picked up and pulled into the correct position for this gesture. A variation was used to pull the baby forwards if it clung (ventrally) in too posterior a position.

R. Cling to ventral surface, cling incompletely to ventral surface.

(33) Hold to ventrum.

D. An extension of the previous gesture. In this case the subject kept its hand applied to the object's back and held it up to its own ventrum.

C. Neonates were supported in this fashion if they clung only with their fore limbs or not at all. Babies were also supported in this way when the subject jumped, descended from a tree or ran swiftly on the ground. The subject progressed with a three legged gait. (Juveniles sometimes held the baby incorrectly using a hand across the neck. In these cases the baby's feet or behind dragged on the ground).

R. Sometimes followed by clinging to ventral surface.

(34) Cling to ventral surface.

D. Subject held onto the object's ventrum. With a standing object, the subject held on well forwards with its head forwards, body slung beneath the object's chest in ventral-ventral contact, and its hands and feet gripping the fur on the object's flanks. As the object sat, or if the subject clung to a monkey already sitting, then the subject often slid down the object's chest and rested in its lap still keeping a hold on its fur with its hands. (Excluded ventral-ventral embrace).
C. The typical way in which young babies clung to another monkey.
R. Carry, relaxation of clinging was followed by ventral embrace
gesture or hold, cradle, look at, teeth-chatter face.

(35) Cling incompletely to ventral surface.
D. Subject (always a baby) hung down by its fore limbs only from
the ventral surface of the object; its feet or behind touching the
ground or waving about. Frequently only one foot was held free.
C. Usually seen when young babies were being carried by their
mothers or very occasionally when carried by juveniles who could
not support them adequately.
R. Ventral embrace gesture, hold to ventrum.

(36) Cradle.
D. Subject sitting with a baby or infant in its lap supported it
with one or both hands across the baby's back, back of head, neck or
chest.
C. Seen in almost every situation where a baby or infant sat in
another's lap. The cradle was particularly used when the baby was
asleep or dozing. The one-handed cradle was frequently used by a
feeding monkey. The pattern is closely related to the ventral em-
brace gesture and the latter often followed cradling.
R. No specific response noted.

(37) On nipple.
D. Baby or infant held nipple in mouth. Attempt to hold nipple
in mouth was also recorded. Only one nipple was used at a time.
It was impossible to tell whether an animal on the nipple was getting
milk.
C. With one exception babies and infants were only seen on their
mother's nipples (i.e. they were consistent in who they sucked from).
The exception involved an orphaned infant on the nipple of a female
that had a baby. Mothers and offspring often sat with their eyes
closed and the babies frequently appeared to be asleep. The nipple
was taken in various ways: (i) Simply sitting in front of the mother. (ii) Lying down beside her. (iii) Squirming under the mother, lifting her arm out of the way. (iv) Leaning over her shoulder (when carried dorsally). On the nipple was frequently preceded by manual manipulation of the nipple.

R. Permitted suckling, cradle, move from, prevent suckling, prevent dorsal carriage, staring open-mouthed pout face.

(38) Manipulate nipple with fingers.

D. Subject, touched, held, pulled or twisted the object's nipple with its fingers. Attempt to manipulate nipple with fingers was also recorded.

C. Seen when a baby or infant was sitting with its mother who was sitting, standing or lying and frequently allogrooming. When a mother was lying on her belly, the subject tried to push its hand under her body towards the nipple or swung under the branch and attempted to reach it while hanging under its mother.

R. Ignore, move from, staring open-mouthed pout face, attack, tense-mouthed face.

(39) Prevent suckling or manipulation of nipples.

D. Mothers used various techniques to prevent or stop their babies and infants from suckling or manipulating their nipples. Some of these patterns are listed elsewhere but are collected here because of their similar function in this instance. (i) Pushed away with hand or forearm. (ii) Rolled onto chest or covered nipples with arms. (iii) Bit or pinched the object's fingers or toes. (iv) Looked at, staring open-mouthed pout face, tense-mouthed face.

C. Seen when object was with its mother (who was perhaps feeding or allogrooming) and attempting to get to her nipples. For instance a baby clinging dorsally to its mother and leaning over her shoulder in an attempt to manipulate or suckle the nipples, was pushed up with the forearm, mildly threatened or bitten. An object that sat in front of its mother and tried to suckle was sometimes pushed away.
R. Cease to suckle or manipulate nipples, looked at, move from, scream, gecker, chup-cheep, bared-teeth gecker face, staring bared-teeth scream face.

(40) **Restrain.**

D. Subject held onto a baby (usually around its waist using both hands) to prevent it moving away.

C. Seen when a young baby attempted to crawl away from another animal. Mothers also held onto their babies to prevent other monkeys from carrying them away.

R. No specific response noted.

(41) **Shake.**

D. Subject holding a baby in its hands shook it up and down vigorously or a subject carrying a baby dorsally shook it by vigorously flexing and straightening its legs and shaking its head.

C. (i) A male seated with a baby in its lap (with or without others sitting with it) would occasionally bend down towards the baby and shake it. Sometimes the baby was held up in the air. (ii) A male carrying a baby would stop (for no apparent reason) and then shake it. In both circumstances shaking was accompanied by teeth-chattering either at the baby, to another monkey seated with it or not directly at any other animal. This behaviour pattern was infrequently seen.

R. Teeth-chatter face; squeaks; usually no specific response noted.

(42) **Touch, grab, pull, push, hold.**

D. Subject put its hand to the object in one of the above ways. Attempt to touch, grab, pull, push, hold was also recorded. (Excluded fighting and other patterns more specifically defined).

C. These patterns were recorded in a variety of (by definition) non-agonistic situations. Examples included: (i) Subject approached a mother with baby, stood by her, looked at the baby and touched it briefly or held onto it gently for some time. (ii) An approach as (i) was followed by the subject grasping the object by a limb and pulling it vigorously. This was usually accompanied by the relaxed
open-mouthed face and often followed by the subject and object playing. In these cases the subject was almost always a subadult or juvenile female and their approach frequently followed vigorous screaming by an infant or baby which was being prevented from suckling. (iii) Subject sitting near object, simply rested its hand on the other's leg, knee or back. (iv) Used during allogrooming to move the groomed into a new position so that another part of the body could be groomed. (v) Babies sitting with older animals often held onto their fur. (vi) When the subject approached an object being carried dorsally and reached and touched it. Following this the object sometimes jumped off. A baby was sometimes removed from the subject's or another's back by pulling it off. (vii) Males allogrooming and with a baby seated near them, frequently reached out and grabbed hold of the baby, pulling it between themselves. This sometimes followed the baby squeaking or screaming.

R. Ignore, look at, relaxed open-mouthed face, play, move from, cease to cling dorsally. When these patterns were directed at a baby or infant with its mother then she sometimes responded by threatening or attacking the subject.

(43) Lift.

D. Subject lifted the object by placing two hands around its waist, by putting one hand under the groin and the other under the neck or upper arm; or by scooping it up with one hand placed under its belly.

C. Examples included (i) Subject picked up a baby with both hands and carried it (shuffling bipedally) to another. (ii) Subject picked up a baby from another's lap or back and then pressed it to its chest using the ventral embrace gesture or hold. (iii) Subject sitting with a baby in its lap, held the baby away from its body, looked at it briefly and then cradled it again. (iv) Two males sitting with a baby occasionally lifted it above their heads, teeth-chattered towards it and sometimes shook it.

R. Squeaks. Usually no specific response noted.
(44) **Pull by thighs (behind-lifting).**

D. Subject gripped the object by the thighs and lifted the object's behind towards itself. The object was usually face down but this was also occasionally done when the object was on its back. Almost always accompanied by the teeth-chatter face or less frequently lip-smacking.

C. A pattern directed towards babies and infants in social interactions involving the subject, object and usually another animal. This is an example of a social signal in which, although the action directly involved only the subject and object, the whole behaviour was stimulated by the presence or action of another animal also present. It should probably be considered as a signal to the other animal rather than to the baby whose behind was being lifted.

Typical situations included: (i) When two males were sitting with a baby between them and one pulled the baby by its legs and the other sometimes by its arm. The males usually bent over the baby and gave teeth-chatter faces and chatter calls. They sometimes mouthed the baby's ano-genital area. (ii) When a female (adult or subadult) approached a mother and her baby/infant she would often sit in front of her, lift the baby's behind and then groom the mother. In some cases contact was first made with the mother, for instance by grooming, and behind-lifting was only seen later. Subadult females frequently lifted the behinds of infants who were calling and attempting to get to their mother's nipple. (iii) A male occasionally approached a baby on the ground, sat behind it and lifted its behind. This should perhaps be considered as a seated mounting. Males doing this were frequently approached by others; only rarely were females seen to use this gesture under these circumstances. (iv) When a mother seated with her baby gave a low intensity threat to a female seated with her, the latter sometimes lifted the baby's behind to her face. If the threatened female had a baby of her own the threatener might follow the threat by lifting the behind of the threatened female's baby.

In the above circumstances the teeth-chatter face was usually directed both at the baby's behind and at the other individual present. In context (iii) teeth-chatters were also given while the
male with the baby looked around at no particular animal. This was not seen in seated mountings with infants and older animals.

R. The babies and infants made little direct response except occasionally squeaking and struggling. Behind-lifting was almost without exception followed by prolonged non-agonistic social interaction between the subject and the other animal present, even if the baby or infant was no longer with them.

(45) Pull by arms.

D. Subject pulled and lifted the object towards itself by pulling its arms or by gripping it under the arm pits. The object was usually face down.

C. (i) Seen less frequently than pull by thighs. Usually only seen when two monkeys were sitting with a baby and as one lifted its behind the other sometimes pulled it by the arms. See the previous pattern for details of context but note it was never seen unless there was a third animal present. (ii) Also seen when the subject was attempting to pull a baby from its mother.

R. As pull by thighs.

8.2.6. Other non-agonistic behaviour.

The following behaviour patterns occurred in a variety of non-agonistic situations. Many of them, however, were also seen during the termination of agonistic interactions.

(46) Allogrooming.

D. The typical grooming behaviour of primates in which the subject parted the object's fur with its hands and picked up particles with either the fingers or mouth. (Plate 8:3)

C. A major non-agonistic activity but it is important to note that the start of grooming was often linked with agonistic behaviour. (See chapter * for details of grooming situations).

R. Monkeys being groomed usually sat or lay in a relaxed posture. Other responses included allogrooming, move from and play.

* see p 214.
(47) Solicitation for allogrooming.

D. It is convenient to group together several postures of similar function. Although also recorded under other circumstances (some have been listed elsewhere in this repertoire) the patterns in the present context were given directly at another individual and appeared to be more stereotyped than similar postures given under other circumstances. They included (i) sitting in front of the object, (ii) sitting upright in front of the object, (iii) laying down on one side, (iv) laying on the ventrum and (v) sitting sideways to the object and bending down in front of it. (See section * for details of postures and context). (Fig. 8.)

R. Allogrooming, solicitation for allogrooming, move to, move from, ignore.

(48) Ventral-ventral embrace (hugging).

D. Subject sat facing the object's ventrum and placed its hands around its body in a hugging gesture. Hugging was often mutual with faces cheek to cheek. (Excluded clings to ventral surface and cradle).

C. Not a frequent pattern. Usually preceded by the subject running towards the object and sitting down in front of it. Typical examples of context included: (i) When juveniles and infants ran towards each other, hugged and then this frequently turned into play involving wrestling and mock biting. (ii) After one adult female had threatened another, the threatener approached, they sat together and hugged each other. (iii) When a female (probably subadult) carrying an infant on its back approached an adult female they hugged briefly before interacting with the baby. (iv) An adult male and juvenile hugged after the former had mounted the latter.

R. Look at, face to head, ventral-ventral embrace, play, allogroom.

(49) Ventral-dorsal embrace.

D. Subject seated behind and in ventro-dorsal contact with the object, placed its arms around the object's body and gripped the fur on its flanks or belly.

* see p 214.
FIGURE 8.1. Solicitation for allogrooming. An infant solicits allogrooming from an adult male. (a) The infant walks near the adult male. (b) Previous to this point there has been no exchange of social gestures. The infant stops and the animals glance at each other. (c) The infant approaches, turns, and lies on its side. The adult bends down and (d) starts to groom the infant. Drawn by Rosemary Deag from 16 mm film by the author.
C. (i) Seen during periods of resting when two or more animals sat in a row each holding onto the animal in front of it. Frequently accompanied by the subject resting its head on the object's back and often followed by the subject grooming the object's back. (ii) Seen when the subject sat behind an object that had a baby or infant clinging to its back or when the object sat in the subject's lap. Usually associated with the subject teeth-chattering, lip-smacking, the subject placing its face to the baby's ano-genital area, and handling the baby.

R. Look at, teeth-chatter face, ignore, allogroom.

(50) Arm under belly/arm over back.

D. Subject stood or sat by the side of the standing object and placed one arm over the object's back and/or the other arm under the object's belly.

C. A rare posture that was accompanied by mouthing the fur on the back and sometimes followed by mounting. It was usually associated with the termination of agonistic behaviour. Examples included: (i) After receiving a threat from an adult female an infant approached her (now lying down), sat by her side and, placing one hand over her body, mouthed the fur on her back and side. (ii) After threatening a juvenile, an adult female ran to its side, sat, placed one hand under the belly and pulled it towards her while placing the other hand on its ano-genital area. The adult female then left. (iii) A subadult female approached an adult female threatening another monkey in a long and vigorous agonistic interaction, sat by her side and placed one arm under her belly and the other arm over her back. The female continued threatening.

R. Look at, ignore, move from.

(51) Arm around back, shoulders or waist.

D. Subject sat or less frequently stood by the side of the object and, facing in the same direction, placed its arm around the object's back, shoulders or waist with or without gripping the fur.
C. Usually only seen when the object had a baby or infant clinging ventrally or cradled in its lap. Frequently preceded by the subject approaching the object and followed by bending the face towards the baby or handling it. The object sometimes reciprocated by returning the gesture. Monkeys approaching a mother and baby in this fashion frequently followed the gesture by grooming her.

R. Look at, teeth-chatter face, arm around back, shoulders or waist, move from, avoid, staring open-mouthed pout face.

(52) In contact.

D. Subject and object sat, stood or lay so that they touched each other without performing any of the other behaviour patterns.

C. Most frequently seen when one animal sat in contact with another during periods of non-agonistic interaction such as allogrooming or resting. Very occasionally a monkey would approach a feeding animal and sit in contact with it. Consorting monkeys sometimes sat in contact after copulation.

R. Look at, ignore, move from.

(53) Face to head.

D. Subject brought its face towards the head of the object and sometimes touched it on the face, side or back of the head.

C. (i) Frequently seen when the subject brought its face towards the head of a baby or infant seated in its own or another's lap. Usually accompanied by teeth-chattering, lip-smacking, slightly pushing the lips out towards the object or pulling the object by the arms. (ii) It also accompanied hugging and was seen on other odd occasions such as when one monkey simply walked up to another and placed its mouth in contact with the object's mouth.

R. Ignore, face to head, ventral-ventral embrace, play.

(54) Head-flagging.

D. The subject moved its head from side to side.
C. Relatively infrequently seen. It sometimes accompanied teeth-chattering but only in situations involving interaction over a baby. Vigorous head-flagging in which the head was swept from side to side was only seen when the subject was really vigorously teeth-chattering or giving the silent bared-teeth face.

R. Head-flagging, teeth-chatter face, silent bared-teeth face.

(55) Ignore.

D. Subject made no apparent response to a gesture directed at it by another monkey.

C. Wide variety of situations. Examples included: (i) When a monkey stood screaming towards another that sat feeding and not looking at the caller. (ii) When a monkey ignored a posture used to solicit allogrooming.

R. This was often followed by the termination of the interaction.

(56) Look at.

D. Subject glanced at the object or looked at it for longer periods. Looking at accompanied most specific facial expressions. There were however numerous situations in which looking at occurred with only the alert face. In these situations looking at differed from 'look apprehensively towards' in which the subject made quick furtive glances and associated intention movements to move from the object. Look at was not restricted to making eye contact.

C. Only cases excluding the more specific facial expressions are considered here. Looking at occurred in every possible context and often as a preliminary to further social behaviour. (i) Looking at was often given without the object noticing the gesture. For instance, as a monkey moved through the feeding group to initiate a group movement many animals would follow it with their eyes. They also looked towards animals calling out of sight. (ii) Many patterns (e.g. postures used to solicit grooming) were preceded by an exchange of glances between the animals.* A preliminary glance between monkeys may permit them to assess each other's mood and so place any following behaviour into context or indeed determine whether any subsequent

* Fig. 8!
interaction occurs. (iii) Particularly intense looking at (not necessarily staring) was a component of intergroup monitoring behaviour. (iv) Looking at (sometimes accompanied by teeth-chattering or lip-smacking) was used to enlist the cooperation of the object against a third monkey.

R. A wide variety of responses remain even if the responses to more specific expressions are excluded. Examples included: look at, look apprehensively at, intention movement to move from, move from, present, teeth-chatter face, bared-teeth scream face, lip-smack face, tense-mouthed face, staring open-mouthed pout face, staring open-mouthed face, move to, solicit allogrooming, allogroom, suckle, ignore.

(57) Look from.

D. Subject glanced away from the object.

C. (i) Frequently associated with look apprehensively towards, intention movement to move from and avoid. (ii) Screaming animals looked both at and away from the object and the latter was used to enlist the cooperation of another against the object.

R. Ignore, staring open-mouthed pout face, tense-mouthed face, teeth-chatter face, lip-smack face, move to, look at.

(58) Look for: search.

D. Subject attempted to find or see another. The searching monkey typically moved its head from side to side or up and down as it looked through the vegetation and these movements were accompanied by crouching or other appropriate flexing of the limbs. At its highest intensity the searching animal moved over the ground and through the trees pausing to examine each tree in turn. This behaviour ceased as soon as the object(s) was located.

C. Seen under two circumstances. (i) When an adult male heard a jabber call, moved towards the source of the calling and systematically searched for the copulating animals. This was usually followed by the subject chasing one or both of the consort pair. (ii) When a mother searched for her baby which was out of her sight and in the
care of other animals. Searching was not usually preceded by screams from the baby; following these calls babies were located without searching.

R. Look at, (i) move from, present, crouch, (ii) move to, clear call.

(59) Play.

No attempt was made to systematically analyse the components of play. A description of play and the contexts in which play occurred is given in chapter II.

R. Play, relaxed open-mouthed face, ignore and (directed towards playing animals by non-participants) the staring open-mouthed pout face.

(60) Hand to own ano-genital area.

D. Subject placed its hand to its own ano-genital area. Females usually reached around the hind limbs; males reached between the legs to touch the scrotum.

C. (i) On rare occasions this accompanied the subject's presentation to an object that had just threatened it. The hand was held to the ano-genital area only briefly. (ii) Also on rare occasions this was given by the subject to a monkey it had just threatened. In both cases it was accompanied by looking at the object. (iii) It was also seen in non-social situations such as masturbation or when a post-parturient female investigated her behind. In the latter case it was followed by olfactory and visual examination of the hand used.

R. (i) Ignore, move to, mount.

(61) Tree-shaking.

D. A monkey shook a tree by bouncing rapidly up the trunk, usually pulling itself up simultaneously with both hands and bouncing onto the trunk with both hind feet together. When it reached the top these movements were repeated several times before stopping. They were also given during a descent. Some shakes were not preceded
by bouncing up the trunk and in these cases the shaking action was sometimes limited to the hands, the feet being held against the trunk. Tree-shaking was performed on live and dead trunks, usually of cedar but also of juniper and oak. When performed on a dead trunk the vibrations produced a loud echoing sound clearly audible in the forest. Vertical trunks were chiefly used but they also shook fallen trunks lodged at an angle against other trees and also horizontal trunks. There was no call associated with this behaviour. (See the sequence filmed by J.H. Crook in Deag, 1970).

C. Primarily seen during intergroup encounters but it was also given at the observer (section 5.6.1).

R. This pattern was a broadcast signal, apparently not directed at any specific individual. Shaking generally had little effect upon the monkeys within the shaker's group and no immediate effect upon the movement or spatial distribution of individuals in other groups (see section 5.6.1).

8.2.7. Agonistic behaviour.

(62) Look apprehensively towards.

D. Subject gave furtive or 'nervous' glances towards the object. Sometimes accompanied (or followed by) intention movements to move from or movement from the object.

C and R. As intention movement to move from.

(63) Stand rigidly.

D. Subject stood on all fours with its limbs straightened and rigid. It was often accompanied by the tense-mouthed face. This posture differed from presenting in the orientation of the body; when standing rigidly the subject faced the object.

C. A preliminary to a running threat or attack by an adult male. As it saw the object it would stiffen and push its head out towards it. Sometimes the interaction proceeded no further. Most frequently seen as a prelude to fight - breaking.
R. Object(s) ceased fighting, look at, move from, present, look apprehensively towards, teeth-chatter face.

(64) Lunge.

D. A graded series of patterns that ranged from thrusting the head towards the object, through flexing the fore limbs and jerking the body forwards, to lunging towards it briefly. Usually accompanied by the tense-mouthed face, staring open-mouthed face, staring open-mouthed pout face, staring open-mouthed pant face, and less frequently with the staring bared-teeth scream face. It was sometimes followed or accompanied by crouching which could be considered as part of the same series of postures.

C. An extremely frequent component of agonistic behaviour. Examples included, (i) when the animals were feeding and one suddenly turned towards another and gave this behaviour pattern. Its onset was stimulated by the proximity of the object or by the object finding a desired food item or water position. This pattern was sometimes subsequently followed by the subject chasing or attacking the object. (ii) Also seen during or after a fight in which the animals lunged backwards and forwards at each other. Under these circumstances it was accompanied by the staring open-mouthed pant face (with pant growls) and the staring bared-teeth scream face (with screams).

R. (i) Almost always followed by, move from, present, look apprehensively towards, intention movement to move from or the staring bared-teeth scream face; and less frequently by crouch, ignore. (ii) Lunge at, the staring open-mouthed pant face, the staring open-mouthed face, growls and the responses listed under (i).

(65) Crouch.

D. Subject flexed its limbs so that its body was lowered towards the ground. When the ventrum was held free of the ground this was termed a half crouch; when it was pressed to the ground, a full crouch. The accompanying patterns varied considerably with the context.
C. (i) Given by a monkey in response to a threatening gesture, chase or attack. It was then accompanied by intense screaming and sometimes defecation. (ii) Given in similar circumstances to lunge at and accompanied by the tense-mouthed face or staring open-mouthed face. (iii) Occasionally seen when a male carrying a baby on its back approached another and crouched in front of it. (See also the dorsal embrace gesture).

R. (i) Move from, ignore, look at. (ii) move from, staring bared-teeth scream face. (iii) As sit sideways.

(66) Attack.

D. Subject hit, bit, pushed, slapped or grabbed object. Attempt to attack was also recorded. Often accompanied by the staring open-mouthed face. (Excluded the pushing and grabbing of babies and infants in non-agonistic contexts, pattern 42).

C. (i) Usually seen following a chase or lunge at the object. Occasionally one monkey sitting next to another would suddenly lash out at it with no preliminary behaviour. (ii) Some of these patterns were used by mothers to prevent suckling. (iii) Mothers seated with their baby or infant sometimes attacked animals interfering with their offspring.

R. Staring bared-teeth scream face, scream, move from, crouch, defecation. On rare occasions the patterns associated with threat and attack were also seen in response.

(67) Bend face towards back.

D. Subject either mounted on the object or engaged in a seated mounting, bent its face towards the back of the object and sometimes mouthed its fur. The mouthing was preceded or accompanied by teeth-chattering, lip-smacking or thrusting.

C. Seen chiefly in non-sexual mountings and seated mountings. Sometimes the mouthing of the fur was very vigorous and best described as biting.

R. Look at, move from, teeth-chatter face, scream.
8.2.8. **Facial expressions.**

The classification used here follows that given by Van Hooff (1967). In the descriptions I have concentrated on the positions of the lips, eyebrows and jaws since these were most readily noted in the field.

(68) **Relaxed face.**

D. Facial musculature relaxed with features in neutral positions, eyes were sometimes completely closed.

C. When engaged in no particular activity. While quietly resting, sleeping or being groomed.

R. No specific response noted.

(69) **Alert face.**

D. Facial musculature under partial tonus with eyes completely open. Mouth closed or almost so and eyebrows in their neutral (unraised) position.

C. Seen with or without eye-contact with another. Typical expression of an active monkey who was looking around, feeding, moving, allogrooming and engaging in most active forms of social behaviour which did not involve the more specific facial expressions subsequently described. Frequently seen in males engaged in intergroup monitoring behaviour.

R. As look at.

(70) **Tense-mouthed face : stare.**

D. This expression corresponded to the description given by Van Hooff (1967) for *Theropithecus* and *Papio*. The mouth was closed or slightly open with the lips concealing the teeth. Eyebrows were raised revealing the paler skin above the eye and beneath the eyebrows. The eyes were wide open and the ears sometimes flattened towards the head. Two main intensities were recognized, in the lowest the eyebrows were simply raised as the subject looked towards the object; at higher intensities it was accompanied by
pushing the face towards the object. In both cases it was frequently accompanied by prolonged looking at the object.

C. (i) The low intensity expression was frequently seen when the subject looked at the observer either casually or for instance during baring, vigilance behaviour or accompanying the up, down and side-ways movements. A clear transition was often seen between this and the two expressions previously described. For instance a monkey resting (with the relaxed face), upon hearing the observer would look up and around (with the alert face) and then look at him with the low intensity tense-mouthed face. In social situations it was given, for instance, by a mother in response to another interfering with her baby, by monkeys to infants playing near them or to a monkey that sat near the subject during travel feeding. (ii) The higher intensity expression was often accompanied by leaning towards the object and was apparently restricted to interaction between the monkeys and rarely given at the observer. It was used in the other situations listed under (i) and also for instance by adult males while standing rigidly (or sitting) and looking towards fighting monkeys.

In contrast to *M. mulatta* (Hinde and Rowell, 1962) and *M. speciosa* (Bertrand, 1969) this expression was not given during an attacking run. Usually the subject was either seated or standing and at the most leaned or stepped towards the object. This is again similar to *Theropithecus* and *Papio* (Van Hooff, 1967). It was almost never followed by attack.

R. Response corresponded to those noted by Van Hooff for *Theropithecus* and *Papio*. They included: look at, look apprehensively towards, look from, move from, teeth-chatter face, lip-smack face, intention movement to move from, ignore, cease fighting, cease playing, present.

(71) Staring open-mouthed face.

D. Mouth open, corners of mouth pulled partly forwards with the lips usually concealing the teeth. Eyebrows raised. The extent to which the mouth was open varied from being almost circular to slit-like. The latter may be considered as transitional
between this expression and the tense-mouthed face. The expression was invariably accompanied by pushing the head out towards the object, lunging, running towards the object and sometimes with growls.

C. (i) Frequently seen during travel-feeding when the subject ran at the object which was close to it. This usually seemed to be simply a response to the close proximity of the object but the subject sometimes assumed feeding or drinking in the position vacated by the object. (ii) Seen in more or less all other agonistic situations (See chapter 10) except usually in response to playing infants or a monkey interfering with a female's baby. The staring open-mouthed face was followed by attack more frequently than the tense-mouthed face.

R. Move from, staring bared-teeth scream face, scream, crouch, defecate, present, teeth-chatter face.

(72) Staring open-mouthed mouth face.

D. Lips protruded and the corners of the mouth pulled forwards to give a small, more or less circular hole between the lips. The teeth were not visible, the eyebrows were raised and the cheeks puffed out to a variable extent. This expression was usually given by a seated monkey and associated with pushing the head and shoulders out towards the object.

C. Typical situations included: (i) Adult animals giving this expression to infants and babies playing near by. (ii) In response to an approach by a baby. (iii) To an animal feeding or standing near the subject. (iv) Following an approach by the object carrying a baby to the subject and (v) By an adult male consorting with an adult female to a subadult male who tried to approach the female. This expression was most frequently directed at babies and infants. It was almost never followed by attack.

R. Look at, move from (usually only a pace or two), intention movement to move from, ignore, lip-smacking face, teeth-chatter face, look from.
(73) Staring open-mouthed pant face.

D. Mouth open (to a variable extent) with lips slightly retracted showing the tips of the teeth. Usually accompanied by lunging towards or backing away from the object, pant-growls and growls. The facial elements were therefore somewhere between the staring open-mouthed face and the staring bared-teeth face.

C. This expression usually followed the other expressions and gestures used in agonistic behaviour. For instance, after one monkey gave the staring open-mouthed face to another or chased it they would sometimes face one another, give this expression and alternately lunge towards each other and retreat. This behaviour usually only occurred between animals relatively close in the social hierarchy. The expression was also given under the other circumstance noted for growls and pant-growls. It was often followed by chase or attack.

R. Staring open-mouthed pant face, move from, move to, present, growl, pant-growl, scream, staring bared-teeth scream face, chase, attack.

(74) Staring bared-teeth scream face.

D. Mouth wide open, lips completely retracted so baring the teeth. Usually accompanied by flight, (or after the initial flight) turning to face and sometimes approach the subject, screaming and occasionally defecation.

C. (i) Given in response to an attack or threat (the sequence of postures and expressions used to define threat is given in section 10.1.2). Occasionally also given when the subject avoided the object without the latter having given any threat. A monkey standing and giving this expression usually looked alternately at the object and away from it even if there were no others near. Prolonged glances were made at higher ranking individuals, if these were near, and this sometimes had the result of enlisting them to form a coalition against the threatener. Animals giving the expression in this context also ran to other individuals and groomed them. (ii) Given by infants and babies when prevented from suckling and in almost all the other circumstances detailed later for baby and infant screams.
In these young animals the facial skin was often screwed up during this expression. The expression was not separated from the furrowing bared-teeth scream face (Van Hooff, 1967). In babies and infants this expression was frequently associated with the bared-teeth gocker face.

R. Ignore, move from, move to, mount, teeth-chatter face, (and infrequently, staring open-mouthed pant face, staring open-mouthed face, chase, attack).

(75) Lip-smacking face.

Van Hooff (1967) called this pattern in *H. sylvanus* the "chew-smacking face" and described it as an expression in which "the under-jaw is moving up and down rapidly (the molars can be heard to meet), the lips remain pressed together and slightly rolled inwards". This expression was seen but "true lip-smacking" (with the lips separating and closing and making a smacking noise distinct from that of teeth-chattering) also occurred. The "tongue-smacking face" involving repeated protrusion of the tongue was only rarely seen. While lip-smacking the eyes were open and the animal looked at the object.

This expression and the following two formed a series that corresponded to an increase in arousal; lip smacking was observed to change to teeth-chattering (noted also by Van Hooff) and the latter to the silent-bared teeth face combined with head-flagging.

C. (i) A variety of non-agonistic situations involving the approach of one animal to another. Examples included: An infant approaching its mother lip-smacked as it sat near her, she looked at it; as a mother collected her baby that had been screaming she lip-smacked to it; as a consorting male and female approached each other they lip-smacked; as part of the dorsal embrace gesture; a male approaching another male with a baby sometimes lip-smacked instead of the more usual teeth-chatter face. (ii) Non-agonistic situations involving two or more animals in close contact. Examples included: A male seated with a baby on its back sometimes looked over its shoulder and lip-smacked at it; Males interacting with a baby between them sometimes directed lip-smacks to each other and the baby instead of the more frequent teeth-chatter face; Males gave this expression
when inspecting the ano-genital region of a female or when copulating; groomers sometimes gave this expression. With them it was frequently mixed with chewing movements as the animals apparently chewed food from their cheek pouches. (iii) In agonistic situations; some threats were followed by the threatened animal lip-smacking at the threatener. The expression was also given by some mounters during seated mountings.

D. The lips were withdrawn to reveal one or both rows of teeth and the lower jaw was moved up and down repeatedly. The meeting teeth gave a chattering noise audible at over 20 m. Really vigorous teeth-chattering was sometimes accompanied by head-flagging and, under some circumstances, by chatter calls. The expression was given facing the object, with the subject's face towards the object's back or ano-genital area, or directed skywards or around and apparently not at any other animal. When a baby was being held or carried it was sometimes accompanied by shaking. (See pattern 75).

C. Agonistic interactions. (i) In response to threat or attack or accompanying passive avoidance. A monkey that avoided another in agonistic situations (with or without a threat or attack being given) sometimes turned to face the object (or presented) and teeth-chattered. Monkeys being chased would similarly turn and teeth-chatter. In this context it was usually followed by the object taking no further action, mounting or inspection of the ano-genital area. The subject occasionally followed this expression by approaching the object. (ii) Monkeys that had been threatened or attacked usually looked around while screaming and glanced at nearby animals. These screams were sometimes followed by teeth-chattering to another animal, which in some cases joined the subject in a coalition against the threatener. (iii) A monkey that had threatened another occasion ally followed this by teeth-chattering at the threatened animal. This was sometimes followed by the object approaching the subject. Bystanders to agonistic interactions on rare occasions teeth-chatter ed to the participants.

Interactions involving babies and infants. (iv) Monkeys picking up, sitting with or carrying babies were seen to look at the baby and
teeth-chatter towards it. When a monkey carrying a baby on its back teeth-chattered to it over its shoulder this, in at least some circumstances, seemed to prevent the baby from jumping off. Teeth-chattering was a component of the dorsal embrace gesture. A monkey seated cradling a baby in its lap occasionally looked around (apparently at no other monkey) and teeth-chattered. (v) Accompanying the removal of a baby from its mother. A male seated with a mother and pulling at her baby in an attempt to hold it and carry it from her would teeth-chatter towards her. If she resisted and increased her hold on the baby the teeth-chattering usually became more vigorous. Animals taking a baby to the baby's mother also teeth-chattered to her. (vi) When carrying a baby to another male. A male that carried a baby to a higher ranking male often approached teeth-chattering or started to do so as it stood facing or across the other. If the subject had the baby on its back then it often also looked over its shoulder and teeth-chattered at the baby. The approached male usually looked at the subject, handled the baby or ignored the approach. When males approached each other rapidly in the presence of a baby the expression was often accompanied by chatter calls. (vii) When interacting over a baby or infant, males sitting with a baby or infant between them gave numerous teeth-chatter expressions. These were directed at the baby (face or behind), each other, the baby's mother (if present), or up into the air or to the side. Vigorous teeth-chatters under these circumstances were sometimes accompanied by head-flagging and on rare occasions, when the animals appeared to be highly excited, the expression was transformed into the silent bared-teeth face with vigorous head-flagging. Mothers with babies teeth-chattered to animals sitting with them. Behind-lifting of babies and infants (by males and females) was usually accompanied by teeth-chattering towards the behind and was followed by grooming the mother or by one male grooming another.

Preceding an approach. (viii) When a monkey approached a subgroup it sometimes stood some way off looking towards it and teeth-chattered. Depending upon the response it received it either joined the subgroup, stayed where it was or left. It was not always the approacher that teeth-chattered; an animal in the subgroup (usually an adult female)
sometimes teeth-chattered towards it and it would then approach.

Associated with sexual behaviour. (ix) Males looking at a presenting swollen female or copulating with one, teeth-chattered.
Copulating females also teeth-chattered to the male either during thrusting or after giving jabber calls.

During non-sexual mountings. (x) The mounting animal in non-sexual mounts often bent its face towards the object's back and teeth-chattered. It was sometimes accompanied by mouthing the object's fur. During seated mountings it was directed at the object's behind. This was also the case when a single male gave a seated mounting/behind-lifting to a baby but it was then frequently accompanied by looking around. In seated mountings it was often followed by the object grooming the subject.

This expression was also given under other circumstances. For instance an adult male passing near a subadult male teeth-chattered towards it. The latter ran to the adult sat with it and mouthed the fur on its shoulder and chest.

R. This was an extremely important and frequent expression. Some responses have been included above. This expression was almost never followed by threat or attack by either subject or object. It was usually followed by approach (or remaining close) and non-agonistic interaction.

(77) Silent bared-teeth face.

D. In this expression the teeth were revealed in the same manner as in the teeth-chatter face but without the associated jaw movements. The teeth were either held together or a short way apart and the expression was accompanied by vigorous head-flagging. Animals giving this expression sat facing the object. (See pattern 75).

C. A rare expression, seen only during close interaction between animals in the presence of a baby or infant. It usually followed a period of vigorous teeth-chattering (context vii above); the teeth-chatter expression was transformed into the silent bared-teeth face simply by stopping the jaw movement. In contrast to some species (Van Hooff, 1967) this expression was not associated with the staring bared-teeth face.
R. Always followed by further close non-agonistic interaction, teeth-chattering, silent bared-teeth face, arm around back, shoulders or waist, behind-lifting, allogrooming, look at.

(78) Bared teeth-gucker face.

D. Mouth slightly open, lips partially retracted, corners of mouth retracted, with the tips of the teeth either just visible or not visible at all.

C. and R. An expression given by babies and infants in association with gucker calls. Details of context and response are given under that heading.

(79) Relaxed open-mouthed face.

D. Mouth wide open with the upper lip tight over the upper tooth row (and usually concealing this) and the lower lip slightly retracted revealing the lower teeth. The eyes looked towards the object and were partially closed. Eyebrows were in the neutral position.

C. An expression always associated with play. (i) A major component of the postures used to initiate play. For instance, one animal would approach another using this expression and a bouncing gait and either reach out towards it (if the object was facing the subject) or grab hold of one of its limbs and pull it towards itself. (ii) The expression was given by animals who were actually playing with others. It was frequently accompanied by gently biting the object.

R. (i) Was frequently followed by play. When the animal initiating play approached the object from behind then the expression was not visible until the object had turned round in response to being pulled by the subject. The object did not always respond to these gestures and mothers frequently threatened animals that did this to their offspring sitting with them. The object often responded with the play face and while playing (ii) both animals frequently gave the expression simultaneously.
8.2.9. Calls.

Calls were recorded, whenever possible, at 19 cm/sec. with a Uher 4000 L tape recorder using a Grampian DP4 microphone fitted to a 60 cm parabolic reflector. The parabolic reflector was fixed to a tripod and details of callers and associated behaviour were written down while recording was in progress. These recordings were supplemented during other observations with a Uher microphone and at a variety of speeds. A selection of the better recordings were analysed, either completely or in part, with a Kay 'Missilyzer' spectrograph.* The number of calls analysed were as follows: barks (8), growls (17), jabbers (24), chatters in situations involving babies (10), screams by juveniles and older animals (26), purrs (3) and other baby and infant calls (42).

As with other macaques (Rowell, 1962; Bertrand, 1969) many of the calls form part of a continuous system; a larger sample would be required to reveal their full variability. For this reason and because the measurement of features on sonagrams can be problematical (Bertrand, 1969) the figures given in table 8.2 should be taken only as a guide. Bertrand divided the calls of *M. speciosa* into:

"Non-tonal, which are developed over a wide range of frequencies; and tonal which have a fundamental and harmonics, and thus possess a definite pitch".

"Non-tonal sounds may be voiced or non-voiced. They form columns of 'white' noise or have a sort of underlying harmonic structure, with large frequency bands distinct from one another. Some sounds possess both structural types".

"Tonal sounds may be pure, mixed with noise superimposed on the harmonic structure and, less frequently, compound with a tonal part followed or preceded by a non-tonal one. A few sounds show all intermediates, from pure harmonics to harmonics almost completely obscured by noise". (Bertrand, 1969 p. 233 to 234, using some terms defined by Struhsaker, 1967).

These comments apply to the calls of *M. sylvanus* and this classification is used here. The analysis focuses on the call units (sounds separated or more or less separated, from preceding and following sounds when the duration of the sonagraph sample was 0.8 sec.) and also upon how the units were built into the complete call. Single call units were rarely given. To help the reader visualize the calls

* Figs. 8.2 to 8.7.
<table>
<thead>
<tr>
<th>CALL</th>
<th>WHITE NOISE</th>
<th>STRUCTURED NOISE</th>
<th>TONAL MIXED OR COMPOUND</th>
<th>INTENSITY (low, medium, high)</th>
<th>DURATION OF UNIT (Secs.)</th>
<th>FUNDAMENTAL OR LOWER FREQUENCY OF ENERGY CONCENTRATION (kHz)</th>
<th>UPPER LIMIT OF ENERGY CONCENTRATION (kHz)</th>
<th>UPPER LIMIT (kHz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bark</td>
<td>x</td>
<td>x</td>
<td>L-H</td>
<td>0.4-0.7</td>
<td>1-3</td>
<td>7</td>
<td>15+</td>
<td></td>
</tr>
<tr>
<td>Growl</td>
<td>x</td>
<td>x</td>
<td>M-H</td>
<td>0.2-0.9</td>
<td>B=2</td>
<td>4-6</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Pant-growl</td>
<td>x</td>
<td>x</td>
<td>L-M</td>
<td>&lt;0.1-0.3</td>
<td>1.5-2</td>
<td>3.5-6</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Screams - all ages</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type 1</td>
<td>x</td>
<td>x</td>
<td>M-H</td>
<td>0.1-2.1</td>
<td>2</td>
<td>6-7</td>
<td>15+</td>
<td></td>
</tr>
<tr>
<td>Type 2</td>
<td>x</td>
<td></td>
<td>M-H</td>
<td>0.1-0.7</td>
<td>5</td>
<td>11-14</td>
<td>15+</td>
<td></td>
</tr>
<tr>
<td>Type 3</td>
<td>x</td>
<td></td>
<td>M-H</td>
<td>0.2-0.3</td>
<td>2-3</td>
<td>4.5</td>
<td>15+</td>
<td></td>
</tr>
<tr>
<td>Type 4</td>
<td>x</td>
<td>x</td>
<td>M-H</td>
<td>0.3-0.8</td>
<td>2.5-4</td>
<td>4-7</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>Type 5</td>
<td>x</td>
<td>x</td>
<td>M-H</td>
<td>&lt;0.1-1.3</td>
<td>0.1-5</td>
<td>8-10+</td>
<td>15+</td>
<td></td>
</tr>
<tr>
<td>Type 6</td>
<td>x</td>
<td></td>
<td>M-H</td>
<td>0.1-7</td>
<td>3-5</td>
<td>6</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Jabber</td>
<td>x</td>
<td></td>
<td>M</td>
<td>&lt;0.1-0.3</td>
<td>Usually B but also 1.5</td>
<td>5</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Chatters</td>
<td>x</td>
<td>x</td>
<td>L-M</td>
<td>&lt;0.1-0.2</td>
<td>Usually 1-2 but also B</td>
<td>2.5-3 but exceptionally 6</td>
<td>10 (15+ in infants)</td>
<td></td>
</tr>
<tr>
<td>Gecker</td>
<td>x</td>
<td></td>
<td>L-M</td>
<td>&lt;0.1-0.2</td>
<td>2</td>
<td>5-8</td>
<td>15+</td>
<td></td>
</tr>
<tr>
<td>Chup</td>
<td>x</td>
<td></td>
<td>L-M</td>
<td>&lt;0.1-0.1</td>
<td>2-3</td>
<td>6-8</td>
<td>15+</td>
<td></td>
</tr>
<tr>
<td>Cheep</td>
<td>x</td>
<td></td>
<td>L-M</td>
<td>0.1-0.2</td>
<td>3-5</td>
<td>6-7</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>Purr</td>
<td>x</td>
<td></td>
<td>L</td>
<td>0.2-1.1</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>

** Measurements give general range of characteristics. 3 calls are not included on this table.  * B = baseline.**
each call is introduced with a brief statement of context; the
definition of the behaviour pattern is still however in terms of
its structure. The relationship between different calls is shown
in fig. 9:8 and discussed after pattern 90.

(60) Barks.
The alarm call of the species.

d. These calls varied considerably in structure. In most cases
the greatest range of frequencies and most energy were concentrated
in the first 0.2 seconds of the call. The mouth opened and shut
for each unit. The eyebrows were sometimes raised. Major sources
of variability were: (i) The extent to which harmonics were develop-
ed. (ii) Vigorous ('complete') units with the mouth medium to wide
open lips not drawn back but teeth visible, graded into low intensity
('incomplete') units given with only a small opening of the mouth and
with little effort put behind the call. Both showed various degrees
of harmonic development but a complete comparison is difficult since
with the more feeble incomplete calls it was harder to record and
demonstrate spectrographically the higher harmonics. In the field
incomplete calls sounded lower and shorter. (iii) The extent to
which units were grouped together and the total length of the call
(sections 7.2.1 and 7.3.1). Calls frequently started with a rapid
series, one unit immediately following another (especially if a
predator was close or attacking) and later settled down to a rate
of 4 - .1 per minute or even 1 per minute. There were often up to
several dozen units per call. Incomplete calls were given in
clusters of 1 - 4 units or mixed with complete units.

c. a call almost unique to the sighting of a predator or potential
predator. Complete calls were given when there was an element of
surprise or uncertainty or if the predator was approaching the group.
Incomplete calls occurred towards the end of the bout of calling and
in habituated groups these calls were given at the observer. In
the latter case the casual nature of the calling was reflected in
the small number of units given and the minimal response of other
animals. Many bouts of calling at predators included both types
of unit and really vigorous barking was often accompanied by growls.
All age-sex classes except babies gave this call.
R. Looking towards caller, flight and ascent of trees, looking towards the cause of the disturbance, barking, ignore (especially in the case of incomplete calls). Additional details on context and response are given in chapter 7.

(81) Growls.

Calls given when threatening and attacking and also at predators.

D. A graded series of calls in which variability was expressed in the length of the unit, the energy put into it and the lower frequency of energy concentration. Two main types are described but intermediates were common.

Basic growls. In these the energy was more or less evenly spread over the length of the unit and the frequency of high energy concentration was either at baseline level or between that and 2kHz. The call was made with the staring open-mouthed face and tense-mouthed face and given with a slight undulation of the jaw.

Pant growls. Shorter than basic growls and with most of the energy concentrated in the first 0.1 - 0.15 sec. The lowest frequency of high energy concentration was 1.5 - 2kHz. Some calls were so soft that they were hardly audible even at close range. The call was made with the staring open-mouthed pant face and associated with lunging towards the object, standing facing it or backing away from it.

Various intermediates between pant and basic growls were associated with intermediate degrees of aggressive behaviour. Some growl calls started or finished with chatter units probably similar to those associated with screams.

C. (i) Basic growls were given by a 'confident' monkey chasing another or running towards it in threat. If the monkey being chased escaped up a tree then the chaser often sat under the tree, looked up and continued calling; this was particularly frequent during flight-breaking. They were sometimes given in response to screams by a monkey in another part of the group. (ii) Pant growls were given by monkeys who were either standing threatening another or backing away from it; they were not given during actual attacking
runs. (iii) Growls were also given at predators and were particularly frequent when the group was being chased by a dog or jackal and followed an initial period of barking. Two adult males that ran at me threateningly made this call. They were also given at birds of prey.

R. Responses to these calls varied with context. Basic growls were followed by flight of the recipient; pant growls were not. Pant-growling was usually mutual with two animals facing each other, calling and lunging backwards and forwards.

(82) Screams.

(1) Juvenile and older animals.

Calls given in response to threat or attack.

D. Screams included a complex variety of units with numerous intermediates. Scream units were classified as follows:

Type 1. (Harsh screams). Units that showed no (or almost no) harmonics. Adult male screams were usually composed entirely of these units and provided examples of the longest and harshest units.

Type 2. Units with numerous well developed close harmonics and some unstructured noise. They often started and ended abruptly with the energy distributed along the length of the unit.

Type 3. Units of short, well developed harmonics followed by poorly structured noise. The harmonics frequently had a ∩ form and a duration of < 0.1 sec. In the noise part of the unit most energy was concentrated in the lower frequencies.

Type 4. (Bridge screams B*). Units in which the harmonics were most distinct (and sometimes ascending) at the start of the unit but later became indistinct in an area of white or poorly structured noise. If harmonics remained throughout the call they were horizontal and not descending at the end of the unit. Few examples of this type were available.

Type 5. (Bridge screams A*). Units composed of narrow, clear, widely spaced harmonics that frequently ascended and descended at

* Terms used by Bertrand (1969).
the start and finish of the unit respectively and started and/or finished in noise. The harmonics in these units were longer than those in type 3 and higher than those in type 4.

Type 6. (Clear screams). Units as type 5 but occurring on their own and with almost no associated noise. The harmonics of these units were intermediate in length between those of type 3 and those of types 4 and 5.

The intermediates that have been identified are given in fig. 3.8; a larger sample might well provide others. Several types of scream graded into chatter units, the transition from clear scream to chatter being particularly abrupt. Scream units were always given as part of a call of 4 to at least 23 units and often lasting up to 15 seconds. The whole calls were very variable and the current small sample makes it difficult to completely relate this variability to context. Since screams were almost entirely given in response to a threat or attack much of the variability probably reflected the intensity of the attack and the way in which this was interpreted by the caller. For instance, some low intensity threats were followed not by screaming but by a series of chatter calls reminiscent of the end of screams - a low level response. Other low intensity threats were followed by a series principally composed of short type 1 units. Really vigorous screaming included principally types 1, 2, 4 and 5 in varying proportions. In adult male screams only type 1 units were recorded and other age-sex differences probably exist. Screams started and finished with all types of unit. Some screams (like the adult males') were very uniform and involved a repetition of one type of unit, others involved a complete variety and also chatter units. At present these differences cannot be explained. Screams were made with the staring bared-teeth scream face.

C. Screams were almost entirely given in response to threat, chase or attack. The screaming monkey would, except in the case of continuing chase or attack, stand or crouch facing the object or move towards it. Looking at the object was frequently interrupted by enlistment glances. Monkeys showing passive avoidance screamed on rare occasions.
R. Ignore, move from, look at, solicit allogrooming, move to, present, teeth-chatter face. Screaming animals were rarely threatened or attacked. Animals not initially involved in the interaction responded to screaming by looking at the participants, growling, running to the fight, fight-breaking or other forms of participation.

(ii) Screams by babies and infants.

Calls given in a variety of stressful situations including rejection by the mother, isolation by a predator and being out of the company of other animals.

D. The scream units were similar to those described for older animals. They probably showed more variation in the structure of the units and had the higher frequencies better developed. Scream types 1 to 5 were identified and intermediates observed including one between types 2 and 5 that was not recorded in older animals. There was considerable variation in intensity; really vigorous calling frequently included types 2 and 5 and, as with older animals, type 3 units occurred as calling died down and was transformed into chup or gecker units. The sample was inadequate to investigate the relationship between type of unit and context. Screams were often extremely lengthy; when denied the nipple or left on their own (babies only) the calling persisted for several minutes and involved rapidly repeated units. A baby left on its own called at a rate of 1 - 1½ units per second; with these relatively long units this meant that there was only a brief break between them. Various degrees of mouth opening were seen; with vigorous calls the mouth was well open and the lips drawn back to show the teeth.

C. (i) This call was probably most frequently given by an infant being denied the nipple by its mother. The intensity of calling varied. It was also given in response to loss of contact with the mother for instance as she moved slightly or left the baby or infant. Also given by a subject running towards the mother in neither of the above situations. (ii) A baby left on its own by another monkey (including its mother) or having itself left another, often gave particularly vigorous calls. (iii) They gave similar calls
when isolated in a tree by the observer (section 7.2.3). (iv) Babies being handled by males during male-baby-male interactions or pulled from their mothers occasionally screamed. (v) Infants screamed when threatened in typical agonistic situations or, more unusually if another prevented them from approaching their mothers. The call was given by an infant apparently frustrated by being unable to reach water in a tree-hole.

R. Permit suckling, prevent suckling, move to, move from, ventral-ventral embrace, cradling, look to, chatter, pull, relaxed open-mouthed face.

Monkeys usually looked towards babies and infants which were screaming. If the screamer was isolated by the observer then an adult male or female frequently moved towards the caller and sometimes carried it to safety. Under other circumstances babies on their own and screaming were usually quickly approached by most age-sex classes and either carried or cradled; screaming sometimes continued until the baby was actually back with its mother. Occasionally other animals clearly ignored the calling and only after several minutes of really vigorous calling was a baby collected. When screaming was a result of the mother preventing suckling, subadult and juvenile females frequently approached and attempted to initiate play with the infant. One subadult male regularly approached a baby under these circumstances and carried it from its mother.

(83) Chups and cheeps.

Calls chiefly associated with loss of contact with the mother.

D. There was considerable variation in these calls but they were all basically tonal.

Chups. Brief calls of variable harmonic development from a full range of clearly developed harmonics to a fundamental and single harmonic. In some the harmonics were relatively close together and separated by noise; spectrographically these looked more like geckers.

Cheeps. Other units had a relatively drawn out fundamental giving a cheep sound. Typically they had no true harmonic development but in some there were oblique pulses of sound above and below the fundamental.
SONOGRAMS OF CALL UNITS - FIGURES 8.2 to 8.7.

Unless otherwise mentioned, recording and analysis details were as follows: Recording speed 19cm/sec. At this speed the frequency response of the recording equipment (p191) was 40 - 20,000 Hz (manufacturer's specification). (At recording speed 2.4 cm/sec (15/16 ips.), frequency response was 40 - 4,500 Hz). The spectrograph was set to give a frequency range of 150 - 15000 Hz with a band - width filter of 60 Hz (both manufacturer's specifications). The duration of each analysed sample was 0.8 sec. The scale given in the bottom left hand corner of each figure is as follows: vertical scale = 10 kHz; horizontal scale = 0.25 secs. Other scales are specified in the captions. Unfortunately there was considerable low - frequency noise on the equipment and also wind noise. This usually appears on the sonograms as a uniform low-frequency band and it should be ignored.

FIGURE 8.2 SONOGRAMS OF BARKS. All except (6) and (8) are 'complete' bark units. (1-3) juvenile male barks on the approach of a man. (4-6) adult female barks at the observer. Part of a sequence given when the female had looked without success for her baby; (6) is an example of an 'incomplete' bark unit. (7) juvenile male barks. (8) Adult female barks. An example of an 'incomplete' bark unit; her mouth was hardly open.

FIGURE 8.3. SONOGRAMS OF GROWLS AND SCREAMS (1) two pant growl units by a juvenile male during an agonistic sequence. (2) two pant growl units directed at the observer by an adult male during an agonistic sequence. (3) basic growl by an adult female. She had chased a subadult male and was sitting looking at him. (4) basic growl by an adult male or an adult female. (5) basic growl by an adult female and a juvenile male's scream in response to this. (6) basic growl by an adult female as she ran in to chase a subadult male. The start of his scream in response to this behaviour appears on the right. (7) Type 1 scream units by a juvenile female being threatened away from a subadult female's proximity. (8) Type 1 scream, probably by a juvenile female.
FIGURE 8.4. SONOGRAHS OF SCREAMS BY JUVENILE AND OLDER ANIMALS. (1) type 2 scream by an adult female who was threatened and chased by a subadult male. (2) type 3 scream units given by an adult female who had copulated, jabber called and then screamed. (3) type 5 scream by a juvenile male being chased by an adult female. (4) type 4 scream by a subadult male in response to an adult female running at him and giving basic growls. (5) type 6 scream by a juvenile male being threatened by an adult female. (6) type 6 scream. Same situation as (3). (7) a particularly complex scream unit made up of several different types of unit. Same situation as (3).

FIGURE 8.5. SONOGRAHS OF SCREAMS BY BABIES AND INFANTS. (1) type 1 scream by an infant female who was isolated in a tree by the observer. (2) type 2 scream by an infant. (3) type 3 scream by an infant female being prevented from suckling by its mother. (4-5) type 4 screams. Same situation as (3). (6) type 5 scream by a 15 week baby male who was alone in a tree (not isolated by the observer). This is an example of the most vigorous units from this scream. (One unit plus the start of the next is shown). (7) type 5 scream by an infant male who was isolated in a tree by the observer. (Note the wide band of wind noise).

FIGURE 8.6. SONOGRAHS OF CHUPS, CHEEPS, CHATTERS AND GEECKERS. (1) Chup given by an infant soliciting grooming from its mother. (Given with cheeps.) (2) chup given by an infant as it huddled to its mother's chest and she groomed it. (3) chup by a baby. This unit is intermediate with the geeker unit that followed it. (4) cheep. A baby female climbed from an adult male's back and ascended a tree. The male left. The baby turned, called chups and cheeps (one of the latter shown here) and descended. (5) cheep given by an infant soliciting grooming from its mother (Given with chups.) (6) cheep by a baby following its mother. (7) series of chatter units given by an adult male when one male was with a baby and two other adult males ran to him in friendly approaches. (Recording speed 2.4 cm/sec; vertical scale = 5 kHz; horizontal scale = 0.25 sec.) (8) two chatter units given by a juvenile male (with an infant clinging dorsally) as it mounted a subadult male. (9) two chatter units given by an adult female when threatened from the proximity of a juvenile male. (10) two
chatter units (the first a chatter; the second a chatter intermediate with a scream) given by an adult female when threatened from the proximity of an adult male. (11) chatter unit given following a scream by an adult female after she was threatened from the proximity of an adult male. (12) chatter unit given after a scream by an infant which was isolated in a tree by the observer. (13) gecker by an infant female following its mother. It was preceded by a cheep. The mother had prevented the infant from suckling. (14) three geckers by an infant running to its mother.

FIGURE 8.7. SONOGRAMS OF SQUEAKS, PURRS AND JABBERS. (1) squeak by a baby (Recording speed 2.4 cm/sec.). (2-3) squeaks by a baby dropping from a branch during play. (The very faint vertical bars are noise). (4) purr by a baby female being carried on an adult male's back. (5) jabber units given by an adult female copulating (with ejaculation) with an adult male. Sonogram shows part of a call made up of many units. (Recording speed 2.4 cm/sec.; vertical scale 5 kHz; horizontal scale 0.25 sec.) (6) two jabber units from the right of (5). (7) jabber units given by an adult female copulating (with ejaculation) with an adult male. This was given on the first mount. One unit and the start of the next is shown.
In all of the circumstances noted below these units were given in short mixed bouts of up to about five units. When associated with screams and geckers they formed part of longer bouts of calling.

C. These calls were given by babies and infants in the following circumstances: (i) When the subject sitting with its mother lost the nipple from its mouth or lost contact with its mother. This occurred, for instance, if she moved slightly, got up or if the subject slipped from her. (ii) When following its mother. (iii) When moving around in her lap, for example, while being groomed. (iv) When pulled by one animal from another's back. (v) It was also given during play, when left alone by an older animal, in response to a mild threat and (rarely) if the observer got too close.

R. Mother moved from it, permitted the subject to gain the nipple or snuggle close. Allogroom, ignore.

(84) Chatters.

Short, sharp units that occurred in a variety of circumstances.

D. Calls from three different contexts are collected together here because (in the present sample at least) the units showed no major differences. There were however context-related differences in the way the units were built into the complete call. The units were in many ways similar to jabbers but with the following differences. In chatters the units usually had most energy concentrated between 1 and 3 KHz and little energy between 1KHz and baseline. The high energy band was (with the exception noted below) almost never divided into harmonics and its upper limit was lower than for jabbers. Chatter units in a series were probably less uniform than jabbers. When chatters followed or preceded screams they were particularly variable showing intermediates between chatters given in other situations and jabbers, growls and screams. They often had high energy more evenly spread over a greater range of frequencies (particularly so in infants) and some tendency for the unit to be divided into broad harmonic bands. A larger sample would probably show continuous variability between these calls.
C. Situations involving babies. (i) When males of all ages (and less frequently females) came together in the presence of a baby or infant then chatter calls were frequently given by one or more of the males. Males removing a baby from its mother sometimes gave chatters as did males sitting on their own with a baby and looking down towards it. It was occasionally given by subadult females approaching a mother and baby. (ii) If a baby that had been screaming was picked up by its mother or another monkey, or if the baby ran to its mother and sat with her, then the surrounding animals looked towards them and gave chatter calls. Most age-sex classes seemed to call in this context. In contexts (i) and (ii) the call was composed of a rapid series of about 5 to 10 units with little space between them. (iii) Chatters were also given in agonistic interactions. They were for instance sometimes given as a short series in response to a threat. They very occasionally accompanied passive avoidance and in both cases this was a low-key response. Some screams started with chatter units and often terminated with a series of units that became less and less scream-like and more and more chatter-like. Chatters also preceded or followed growls; with these the mouth was slightly open with the lips over the teeth. The number of units in a series was more variable than in chatters in situations involving babies.

R. (i) Usually followed by close contact and non-agonistic interaction over the baby or the mother permitting the removal of the baby. (ii) No response noted. (iii) When associated with screams or flight responses included ignore, look at, move from. When associated with growls, see the responses for that pattern.

(85) Jabbers

Short sharp units given by swollen females, chiefly when copulating.

D. With the exception of poorly developed units at the start the units in a call were characterised by their uniformity of structure. The units had a steep attack and most of the energy was concentrated with the first 0.1 - 0.15 secs. of the unit, and below 5kHz. The high energy part of the unit was broken up into broad harmonic
bands, but the extent of this varied between calls. In many there was more or less even development from baseline to approximately 3KHz, in others there was little development in the area 0.5 - 2 KHz. These may represent individual differences. The units were quite constant in length and evenly spaced with 9 to 28 units in a call lasting 2 to 10 seconds. The call was given with the lips pouted and rapid movements of the diaphragm. It was sometimes preceded by lip-smacking and on rare occasions transformed into screams.

C. (i) Given by a female during copulation. Calling usually started during the male's thrusting and became louder either towards the end of this or as the female ran forwards away from him. In many cases she would turn to face him after the copulation, sit and continue calling. (ii) Swollen females either seated on their own or pursuing a male also gave this call. There seemed to be no difference between the calls given in the two situations.

R. During or after copulations no specific response was detected in the male copulating with the caller. Adult males upon hearing this call sometimes looked up and moved towards the source of the sound and looked for the consorting animals. One or both of the pair was then chased, the consort broken and the male often took over the female and consorted with her. Non-consorting callers were occasionally approached and consorting followed.

(86) Geckers.

Calls associated with loss of contact with the mother and other mother-infant behaviour.

D. Columns of white noise of brief duration. (i) In true geckers the energy was spread more or less evenly over a wide band of frequencies usually above 2KHz. There was more energy in the higher frequencies than in either chatters and jabbers; there were however intermediates very similar to the latter. (ii) In some units (gecker-cheeps) more energy was concentrated at the relatively high frequencies and the unit was more drawn out at that point. Some of these looked superficially like cheeps but in the latter the components above and below the energy concentration were slightly obliquely orientated. All geckers were given with a variable number of units together.
C. Given by babies and infants in the following circumstances:
(i) When the subject sitting with its mother momentarily lost its footing and then snuggled into her. (ii) As its mother stopped grooming it the subject sometimes sat up and called. (iii) If it reached for the nipple and was gently pushed away. (iv) When following its mother, especially if she had just got up and left it. (v) When running to its mother or (vi) when climbing over her.

Geckers were frequently associated with screams and chup-cheeps; screams of babies and infants often ended in chup-cheeps which were then followed by geckers.

R. As chup-cheeps.

(87) Squeaks.
Brief tonal calls given by babies.

D. A heterogeneous collection of squeak-like calls all made by babies. The extent to which harmonics were developed apparently varied.

C. While being handled by males; when crawling on the ground near males; during play, for instance while jumping.

R. If with males, these usually turned to the baby and picked it up.

(88) Purr.
Calls usually given by babies when carried dorsally.

D. Very low intensity, low frequency calls in which a brief tonal component with close, narrow harmonics was followed by a slightly wavering component with a very indistinct harmonic structure. The tonal component was sometimes almost absent. The call sounded something like the muffled purr of a cat and was composed of up to several dozen units with a 1-2 second gap between units. Longer gaps also occurred breaking the call up into distinct phrases. (These calls were difficult to hear and record and the sample available for analysis was small).

C. Given by babies when carried on the back of other animals. Typically the baby would run towards the object, leap on and then call with its face held close to the object's back. It was seen
most frequently in babies that had been screaming previous to running

to the object. It was also given when object sat with the baby on
its back or cradled it.

R. No direct response noted.

(89) **Grunts.**

Calls given by quietly feeding monkeys.

D. Extremely faint calls that were probably tonal with little or
no noise. They were difficult to record and no spectrographic
analysis was possible. They seemed to vary in pitch and duration
and in some the pitch rose, in others it fell. Most were given
with the mouth closed but on occasion similar calls were given with
the mouth open, lips drawn back revealing the teeth and no jaw move-
ments. The calls were given in choruses separated by several minutes.

C. As the monkeys were feeding these calls could be heard passing
to and fro across the group. On one occasion apparently similar
calls were given in response to a baby's scream and a clear call.
The calls may help maintain group cohesion.

R. When the animals were quietly feeding much of the calling
appeared to be antiphonal.

(90) **Clear calls.**

Calls apparently given by or at individuals that had become
separated from the group.

D. A high pitched tonal unit probably with little or no noise
that can be represented as 'ese'. Units given singly or in a
short call with (in one case) each unit separated by up to 30
seconds. This call was rarely heard and no satisfactory record-
ing was obtained.

C. It was only seen to be given twice. On one occasion a mother
had spent at least 10 minutes looking for her baby which was in the
care of a subadult female well away from the rest of the group.
As she returned towards the group she called when the mother was
60 m. away; the mother then moved to the subadult female and took
the baby from her. On the other occasion a consort pair had been
left behind as the group moved on. A juvenile male sat looking towards them and called about six times. After the female rejoined the group the juvenile male sat watching the male and did not move back towards the rest of the group until the adult male had done so.

R. On one occasion a clear call by an unobserved animal was followed by most of the group barking and an adult male positioning himself so as to look towards the sound source.

Discussion on calls. Fig. 8.7 shows the known intermediates between calls and groups them together by context. There are three principal points of interest:

(i) Screams given by monkeys, juvenile and older, following threat were clearly related to (in some cases the same as) the calls given by babies and infants when rejected by their mothers, when left on their own or when isolated by predators. Screams may therefore be thought of as calls given in any fearfull or frustrating situation. Screaming babies and infants were not attacked; they were either collected by their mothers (and others) or ignored by their mothers especially when the screaming was associated with the prevention of suckling. In older animals screaming is usually considered as a sign of submission and in the present study was rarely followed by attack. It is probably significant that a signal used to elicit maternal behaviour is used by older animals to indicate submission. Other calls given in fearful situations (e.g. some barks) were also similar to some screams; like chup-cheeps and clear calls they sometimes had tonal components and harmonics.

(ii) Calls given in non-agonistic approaches or proximity were similar and involved brief columns of relatively unstructured noise. Although there were differences in detail it is striking how adult growls and screams started or finished with chatters that were similar to gackers given by babies to their mothers. Jabbers and the remaining chatters, given during close non-agonistic interaction between older animals, were also similar to gackers. They both (especially jabbers) involved gacker like units which were given in a rapid stereotyped series.
FIGURE 8.8. Intermediates between calls, and the contexts in which calls were given. Solid lines link calls for which intermediates are known. S. Type 1 etc. refer to the different categories of screams. Dotted lines enclose calls given in each of the four specified contexts. Calls for all age-sex classes are included. 3 calls are omitted - purrs, clear calls and grunts.
(iii) Many of the linked series of calls in Fig. 8 & 8 represented changes in intensity of calling and other behaviour. For instance:

(a) There was an increasing tendency to attack associated with the transition pant-growl to basic growl. (b) The series in babies and infants, screams—chup-cheeps—gecker-cheeps—geckers was associated with a decrease in the intensity of separation or rejection by the mother. (c) The series, type 3 screams—barks with harmonics—barks without harmonics—growls was apparently associated with an increasing tendency to attack a predator.

8.3. PHYSICALLY DISTINCT BEHAVIOUR PATTERNS WHICH ARE PROBABLY NOT COMMUNICATIVE.

Many of the following behaviour patterns carried information on the state of the animal or its environment but, in contrast to the patterns given in section 8.2, they were only indirectly used in social interactions.

8.3.1. Locomotion.

Diagonal walk.

The typical quadrupedal progression of many primates with the right fore leg moving with the left hind leg and the left fore leg with the right hind leg. It was the principle locomotory pattern on the ground and in the trees. The overall appearance of a walking animal varied with its age-sex class and social rank. All animals moved in a relaxed fashion but in lower ranking animals this varied with the company and at times their walking rhythm was broken by glances at their neighbours.

Fast run or gallop.

As an animal's speed increased the sequence of limb movements changed from those of the diagonal walk to a sequence in which the fore limbs moved more or less together followed by the hind limbs moving in a similar fashion.
Three-legged gait.

A monkey carrying an object in one hand or holding a baby to its ventrum, walked or ran on three legs. Every few paces the animal put the fourth limb to the ground as a brief support.

Hunched walk.

A monkey moved in a hunched up manner with the back slightly arched, taking short paces and with one fore limb sometimes held up to the chest. This was given by only one or two animals (usually infants) at a time on cold, wet or snowy days.

Crawl.

A young baby unable to raise itself up on its hind limbs, pulled itself along on its arms.

Gambol.

Unco-ordinated, bouncing, quadrupedal progression seen in babies. It followed crawling and was replaced by the diagonal walk.

Inverted walk.

The monkey hung underneath a branch with its dorsal surface towards the ground and progressed by moving hand over hand, foot over foot. This was primarily given by infants when their mother was lying on a narrow branch and they were attempting to suckle; it frequently followed the prevention of suckling and was accompanied by vigorous screams.

Climbing and descending.

Climbing commenced with a jump from the ground and catching hold of a branch. It frequently proceeded in a spiral fashion as the animal followed the position of the side branches. The co-ordination of the limbs varied with the speed in a similar fashion to movement on the ground. Fast ascents were punctuated with brief pauses as the animal slowed its pace momentarily and glanced up at the next branch. Less frequently animals started to climb by grabbing hold of a low bough and scrambling up.
Descending animals usually moved head first, jumping down in a spiral fashion. The final drop to the ground was accomplished in one of two ways. In a quick descent they simply continued to descend head first and jumped to the ground; in more leisurely descents they paused on the last branch, lowered themselves by the arms and, propping themselves briefly against the trunk with the hind limbs, dropped to the ground landing more or less evenly on all fours. Young animals occasionally swung by their arms and dropped directly to the ground. Arm swinging was always extremely brief.

Hang by arms or feet.

Arm swinging during descent has just been described. Arm swinging and hanging by the feet were frequently seen in playing babies and infants.

Leaping.

All age-sex classes frequently leapt from tree to tree. A leap was preceded by movement towards the jumping position, a glance towards the other tree and a quick spring forwards powered primarily with the hind legs but also involving a rapid pull with the hands. Monkeys jumping long distances usually landed on leafy boughs. Almost all landings were on trunks or branches out of the vertical; occasionally an animal would land on a vertical trunk in a manner more reminiscent of a prosimian. Long leaps by young animals were sometimes preceded by a careful examination of the jump and they would approach a point several times and make intention movements to jump, before either jumping or moving to another place. Leaping onto solid branches was less frequent when they were slimy or icy. Jumping was also used to clear streams.

Shifting.

Monkeys seated feeding or digging moved short distances by shuffling forwards on their behinds. Compared, for instance, with Theropithecus gelada (Crook and Aldrich-Blake 1968) the time spent doing this was small.
Bipedal standing and locomotion.

This was seen under three main circumstances:

(i) A monkey hearing a noise would stand on its hind legs and look towards the source of the sound. This was more frequently seen on the ground than in the trees. A similar stance was occasionally taken by animals looking towards calling elsewhere in the group. The hands hung by the side.

(ii) Animals standing on the ground reached up into bushes to gather food items. They usually supported themselves with one hand.

(iii) Animals carrying food items (section 6.3.1) sometimes held these to the chest with one or both hands and moved short distances bipedally. A male carrying a baby to another male sometimes carried the baby in its hands for the last few paces and shuffled bipedally. Likewise a male pulling a baby to its chest vigorously and turning to leave a social interaction, often stood bipedally and swung away from the other animals. Associated with this was the pushing out of the free hand high into the air in preparation for the first pace.

8.3.2. Resting postures.

Relaxed sitting.

This was the typical sitting posture of an animal not resting against a support. The back was smoothly curved; the knees bent with the hind limbs drawn up to the body; the fore limbs were either held in the lap, on the substrate between or outside of the hind limbs, or rested on the hind limbs. The feet frequently were rested one on top of the other. During cold weather they sat with the palm of the hands pressed to the chest and the soles of the feet pressed together. The position of the head varied considerably. When dozing it was dropped forwards with the muzzle pointing downwards; when alert but looking around casually the muzzle was slightly raised, and when looking intently as (in intergroup monitoring behaviour) the face looked straight ahead and the muzzle was more horizontal. Relaxed sitting was seen in all age-sex classes. Feeding animals took up a very similar position with the exception that they usually leaned further forwards and sometimes rested on one hand while picking up items with the other.
Upright sitting.

In this posture the back was straighter and more vertical with the shoulders pulled somewhat back. The head was usually looking forwards and the fore limbs either resting on the knees or holding onto a branch. Animals adopting this posture were usually alert and actively looking about. Vigilant animals adopted this and the previous posture. It was less frequently seen in resting animals. Usually seen in subadult and older animals.

Extreme upright sitting (sunning posture).

After taking up a position in the early morning sun (or at other times of the day in winter) they sat in this characteristic posture. The back was vertical and not arched, the shoulders pulled back and the chest pushed out. The neck was stretched upwards with the face pointing forwards or slightly raised. The hands were held by the side or on the knees and the chest directed towards the sun. This was seen in all age-sex classes except babies. Young animals (particularly infants) sometimes adopted this posture while being groomed.

Hunched sitting.

During cold, rainy or snowy weather they often sat with the back strongly arched, shoulders rounded and head down towards the chest. Several animals would huddle together in the dorso-ventral positions described as the chin on nape posture (Bertrand, 1969) or with the chin of one resting on the back of another (nestling, Bertrand, 1969). In the more relaxed atmosphere of a wild group I did not recognize as a separate posture the cat-like or subordinate sitting (Hinde and Rowell, 1962; Bertrand, 1969) commonly seen in low ranking captive animals.

Supported sitting.

A variety of other sitting postures were adopted when they took advantage of branches or rocks to provide support. Examples included (a) sitting with the feet raised on a support with the hands either resting in the lap or against the support. In this
posture the ischial callosities seemed to provide the sole contact between the animal and the object it was sitting on. (b) Sitting with the chin resting on a branch, or the whole body leaning against a support with the head resting on the forelimbs. Adult males dozed in this position.

**Lying.**

A variety of lying postures were adopted. These included (a) lying on the ventrum with the limbs tucked under the body and resting on the elbows. Animals being groomed frequently adopted this posture. (b) As (a) but with the chin resting on the hands. This posture was used while resting in the trees. (c) Lying on the side with the legs outstretched. Used while resting, while being groomed and also to solicit grooming (q.v.) (d) As (c) but with the limbs drawn in towards the body. This was adopted while resting along a branch or when lodged in the fork of a tree. The latter was rarely seen.

8.3.3. Maintenance activities.

**Feeding, drinking, and food preparation.**

See chapter 6.

**Elimination.**

No specific behaviour was associated with elimination.

**Autogrooming.**

Monkeys picked over or brushed aside their own fur in search of items that they put in their mouths. Details of autogrooming are given in chapter *.

**Scratching.**

Monkeys used both fore and hind limbs to scratch themselves; the latter were used to scratch behind the ears in the manner seen in dogs. It was most frequent early in the day and often associated *see p.214.*
with autogrooming and allogrooming. Animals giving intergroup monitoring behaviour and watching the observer occasionally scratched.

**Fly swotting.**

Flies that flew around the monkeys or settled on them were swotted.

**Sheltering.**

They sometimes sought shelter on the leeward side of tree trunks or under branches from driving rain, snow or hail (section 4.5).

**Shake fur.**

Monkeys that had been feeding in the rain cleared water from their fur by shaking like a dog.

**8.3.4. Miscellaneous.**

**Yawning.**

This was seen during a variety of situations almost always non-social ones. Examples included watching the observer, when stared at by the observer, and when resting or giving up, down and sideways movements. Social situations included intergroup encounters and occasionally in association with agonistic behaviour.

**Up, down and sideways movements.**

These movements of the head and body may be social signals since they alert other monkeys to the source of disturbance (see section 7.2.2.)

**Startle reaction.**

A sudden flexing of the limbs and slight lowering of the head; given by a standing animal when startled. This was usually given in response to a loud noise and followed by the animal jumping around to face the stimulus. Animals turning stones occasionally jumped aside in a startled fashion but the cause of this was not discovered.
Carry.

Items carried were chiefly food items or twigs carried by infants and babies during play. See sections 6.3.1 and 7.3.3.

Hide.

One response to the observer was to hide carefully in the branches. See section 7.2.1.

Self-milking.

An adult female took her own nipple into her mouth. Rarely seen. On one occasion, a subadult female who had been attempting to carry a baby from its mother was only permitted to do so after the mother had taken her own nipples into her mouth.

Testicular adduction.

The testes of adult, subadult and older juvenile males were usually descended. On occasions, however, the testes were adducted and the scrotum was either hardly visible (especially in juveniles and young subadults) or the folds of the scrotum clearly seen. During the summer adduction was almost never seen, but was immediately noted when the cold weather arrived. On cold, wet days throughout the winter some or all of the males usually had adducted testes; if it became warmer later in the day then they descended.

Sexual patterns.

It was usually difficult to tell whether intromission and ejaculation occurred in a copulation. A pause at the end of thrusting (Altmann, 1962) or the presence of ejaculate on the female's genitalia was used to score ejaculation. Erection of the penis was observed not only during copulations but also during male-baby-male interactions, allogrooming and non-sexual mountings. Masturbation was infrequent and never resulted in ejaculation. A male sometimes ate the remains of his own ejaculate after a copulation.
Noises.

Noises not associated with social displays included hiccuping, sneezing, vomiting and coughing.

8.4. DISCUSSION.

No detailed comparisons will be made between the behaviour repertoire of this and other macaques. My purpose is to point out those patterns which appear to be either unique to the species (as demonstrated by the study population) or particularly emphasized in this animal.

The following patterns seem at present to be unique: sit sideways, stand sideways (orientation postures have not been discussed by most authors and so their uniqueness may be more apparent than real), sit in lap (it is important to separate this from sit behind and the ventro-dorsal contact seen in nestling), pull by arms, arm under belly/arm over back (this may be a variation of ventral-ventral embrace which is seen in several other macaques), staring open-mouthed pout face (recognized as unique among adult macaques by Van Hooff, 1967) and shake. Chatters (as seen in situations involving babies) are unique in context at least.

The following patterns are definitely found in other macaques but are apparently given with a greater frequency in M. sylvanus and by unusual age-sex classes (e.g. males as well as females) or under special circumstances: pull by thighs (behind-lifting), lift (contexts (i) and (iv) described earlier), arm around back, shoulders or waist (Bertrand, 1969, also noted that this was frequent in M. sylvanus), the teeth-chatter face (also noted as important by Van Hooff, 1967), and the silent bared-teeth face with head-flagging (associated with maintenance of proximity and not fleeing).

It was remarkable that with only two exceptions (arm under belly/arm over back, staring open-mouthed pout face) these patterns were regular components (most of them major ones) of the unique series of social interactions involving babies or infants and males which were discovered in this population. If one assumes that this male-baby-male behaviour (see chapter 12) is of more recent origin than the interactions between a mother with a baby and other females
(described in this and other species of macaque), then one can suggest that the more specialized components of the male's interactions are drawn from three sources: (a) By the inclusion of behaviour patterns (such as the teeth-chatter face) that are seen in other situations to have appeasing, reassuring (as defined by Van Hooff, 1967) or submissive functions.

(b) By the inclusion of elements from the interactions between females and mothers with babies (e.g. arm around back, shoulder, waist; behind-lifting) which are used in this species, M. speciosa (Bertrand, 1969) and probably M. radiata.

(c) By the development of new elements with a specific function. Examples of these are sit sideways, stand sideways, sit in lap and chatter. These patterns are all involved when the males come together in the presence of a baby, presumably a point of potential conflict if few male to male approaches are made at other times. The first three depend on the approacher (carrying the baby ventrally or dorsally) orientating himself to the approached animal and giving gestures such as the teeth-chatter face. Chatter calls are structurally related to other situations involving non-agonistic approaches or contact (Fig. 28), and so it is not too surprising to find them in the circumstances under discussion. The function of these patterns is discussed further in subsequent chapters and it should be noted that some (e.g. chatters) are seen outwith the circumstances noted above.

Most of the patterns used by different macaques in agonistic behaviour are extremely similar and the unique use of the staring open-mouthed pout face in this context is therefore of particular interest.

8.5. SUMMARY.

The criteria used to define the behaviour patterns are discussed. Patterns which are thought to be communicative are defined primarily by their structure and not function; for each pattern details are given of context and the responses of other animals.
*M. sylvanus* has a rich and varied repertoire showing many similarities with other macaques. The calls recognized were part of a matrix of structurally related calls and several transitions between types of call represented changes in the intensity of the signal or the response to a signal. The relationship is discussed between the function of calls given by babies and infants and the function of similar calls given in different contexts by older animals.

The differences between the repertoire of this species and other macaques are of considerable interest since most of the unique or especially developed patterns were major components of the unique male-baby-male social interactions described in subsequent chapters. The species also has a unique expression used in threat.

Non-Communicative behaviour patterns are also described.

**Addendum.** My original intention was to include a detailed analysis of allogrooming. Lack of time has prohibited this and the topic must be reserved for a future report. Comments on allogrooming are as follows:— Description of allogrooming (p172); solicitation for allogrooming (p173); allogrooming and agonistic behaviour (chapter 10); allogrooming between mothers and other females and as a component of maternal and female care (chapter 11); allogrooming between males and in male care (chapter 12); diurnal distribution of allogrooming (p72, 417). See also Deag (1970).
9. INTRODUCING THE STUDY OF SOCIAL INTERACTION

9.1 INTRODUCTION.

The most characteristic feature of any society is the distribution of social acts between individuals. Social behaviour is usually non-random; it is structured, for instance, with reference to the patterns used, their frequency and their distribution between individuals. One of the main aims of this project (Section 1.4.1) was to describe the behaviour within groups. In the following chapters I shall be examining:

(i) The variety of social interactions seen and their components.
(ii) The relative frequency of different categories of behaviour.
(iii) The distribution between individuals (and age-sex classes) of certain behaviour patterns or constellations of these.
(iv) The ontogeny of some types of behaviour.
(v) The significance of some specific types of social interactions.
(vi) The diurnal distribution of social behaviour.
(vii) The relative sociability of individuals.

I believe it is essential in any preliminary study to maintain perspective by sampling a wide spectrum of behaviour; subsequent more detailed observations may then be viewed against the background of the animals' total behaviour. Since randomness of behaviour is not expected it might be considered pointless to compare results with a random distribution. Usually, however, one's aim is not simply to prove non-randomness; if one is interested in the differences between individuals a random distribution provides, in many cases, a convenient baseline to measure from. Higher-level hypotheses, based on studies of similar species, may involve unwarranted assumptions. Direct comparisons between selected individuals or groups of individuals are also used.
In chapter 13 the spatial distribution of group members is investigated quantitatively and the following chapters reveal the importance of individual behaviour in producing such gross distribution patterns. Unless otherwise stated the quantitative results given in subsequent chapters were collected during the single group study of group 6 (Section 1.4.1). It should be noted that the size of this group (25 individuals) was close to the estimated mean group size for the population (mean = 24). Details of group 6 monkeys were given in section 3.3.3.

9.2. DATA COLLECTION.


In the population study data from numerous groups was collected by recording behaviour protocols. These provided details of behaviour patterns and the variety of interactions likely to be encountered during the single group study. With group 6 I was interested in the overall distribution of behaviour within the group and how this was expressed, both in terms of the flow of behaviour shown by an individual and in the linking together of the behaviour of several individuals during social interactions. It was therefore essential to select a recording method compatible with this aim. One technique which provides detailed and accurate data, is to select an individual at random and keep it in view for as long as possible (or for a fixed period of time) while recording its behaviour continually or at fixed intervals. Such data may give a 'complete' record for the selected individual but it gives only brief and incomplete glimpses of social interactions; the behaviour of other individuals is recorded only when it coincides with that of the selected animal. The problem is particularly acute with a large group and with 25 individuals it would also be difficult to accumulate sufficient time samples with each animal.

I therefore chose a method that focused on social interactions and at the same time provided data on the flow of behaviour shown by individuals. In this method the behaviour of all visible individuals was continuously recorded during 'continuous recording sessions'. These lasted from several minutes to several hours and the start
and finish time of each session was noted. During a session the observer continually scanned the area where the animals were visible. In this way the behaviour of visible animals was monitored and other individuals picked up as they came into view. Using this technique the behaviour of individuals both before and immediately after a social interaction could be included in the records. The recording session was terminated if contact with the animals was lost and I either moved around until animals were again visible or waited until animals moved into view. If the participants in a social interaction became obscured by vegetation, I would move a pace or two to get them back into view so long as this did not mean interrupting the recording of other social interactions. Apart from this, the following of specific individuals or social interactions was excluded and I made every effort to avoid biasing the data by concentrating on particular individuals or types of behaviour. The recording of an interaction continued until it finished or the animals moved out of sight. Sessions were terminated if the animals were disturbed by a predator, the observer or intergroup encounters. Breaks in observation were recorded. With only a small portion of the group visible at any one time and a mean data collection rate of one interaction every 27 minutes, the observer was only occasionally swamped with data. To decrease the angle that had to be scanned I purposely did not work as close to the animals as would have otherwise been possible. Observations were made in all parts of the habitat.

Compared to the time-sampling of an individual's behaviour, the continuous recording session technique increased the data collected on complete social interactions but it necessarily decreased the detail that could be recorded. After experimenting with check-sheets I found that the most efficient way to collect data was to dictate notes on to a tape recorder; those visible could then be continuously scanned without interruption. Tapes were transcribed into duplicate books but no data-analysis was attempted until data collection was complete. A total 3192 social interactions were recorded during 146 hours of continuous recording sessions (table 9.1). The analysis was based on a sample of these interactions (Section 9.2.3).
<table>
<thead>
<tr>
<th>SAMPLE</th>
<th>DATE (1969)</th>
<th>DURATION OF C.R.S. (HOURS)</th>
<th>NUMBER OF INTERACTIONS RECORDED</th>
</tr>
</thead>
<tbody>
<tr>
<td>Preliminary sample. Non-mating season</td>
<td>20.5</td>
<td>6.67</td>
<td>75</td>
</tr>
<tr>
<td></td>
<td>22.5</td>
<td>1.70</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>23.5</td>
<td>5.42</td>
<td>98</td>
</tr>
<tr>
<td></td>
<td>24.5</td>
<td>1.00</td>
<td>21</td>
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<td></td>
<td>27.5</td>
<td>4.17</td>
<td>66</td>
</tr>
<tr>
<td></td>
<td>28.5</td>
<td>5.68</td>
<td>85</td>
</tr>
<tr>
<td></td>
<td>2.6</td>
<td>5.12</td>
<td>118</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td></td>
<td><strong>29.76</strong></td>
<td><strong>479</strong></td>
</tr>
<tr>
<td>Main sample. Non-mating season</td>
<td>4.6</td>
<td>3.77</td>
<td>69</td>
</tr>
<tr>
<td></td>
<td>6.6</td>
<td>3.97</td>
<td>65</td>
</tr>
<tr>
<td></td>
<td>7.6</td>
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<td>126</td>
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<td>8.6</td>
<td>0.90</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>1.7</td>
<td>5.53</td>
<td>69</td>
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<td></td>
<td>3.7</td>
<td>3.80</td>
<td>53</td>
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<td></td>
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<td>10.7</td>
<td>7.17</td>
<td>198</td>
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<tr>
<td></td>
<td>13.7</td>
<td>5.98</td>
<td>85</td>
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<tr>
<td></td>
<td>21.7</td>
<td>2.00</td>
<td>46</td>
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<tr>
<td></td>
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<td>8.97</td>
<td>172</td>
</tr>
<tr>
<td></td>
<td>27.8</td>
<td>10.02</td>
<td>271</td>
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<td></td>
<td>1.9</td>
<td>10.03</td>
<td>250</td>
</tr>
<tr>
<td></td>
<td>4.9</td>
<td>8.63</td>
<td>216</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td></td>
<td><strong>77.71</strong></td>
<td><strong>1740</strong></td>
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<tr>
<td>Mating season sample.</td>
<td>30.9</td>
<td>9.58</td>
<td>248</td>
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<tr>
<td></td>
<td>1.10</td>
<td>10.78</td>
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<td>2.10</td>
<td>11.17</td>
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<tr>
<td></td>
<td>3.10</td>
<td>6.58</td>
<td>175</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td></td>
<td><strong>38.12</strong></td>
<td><strong>973</strong></td>
</tr>
</tbody>
</table>

Grand totals 145.59 hours; 3192 social interactions.
The records from continuous recording sessions were supplemented in two ways. In order to increase the sample on the behaviour of babies I introduced additional recording sessions whenever time permitted. During these the major details of the babies' social interactions were recorded whenever they came into sight. The start and finish times of these sessions were recorded so that for some purposes (e.g. in determining the proportion of time a baby spent with various individuals) the additional data was directly comparable with the continuous recording sessions. Incidental notes were made on all types of social interactions whenever these were of interest. These supplementary observations have not (unless specifically noted) been used in the quantitative results given in the following chapters.

9.2.2. Possible sources of bias.

Data collected by the above technique will be more susceptible to bias than data collected by concentrating on one individual at a time. Chalmers (1968a,b) and Aldrich-Blake (1970) discuss the first two of the following points in detail.

(i) Some activities may be more noticeable to the observer than others; fighting may be over emphasized and sitting in contact under emphasized simply because the observer would notice the former more readily. This would affect the apparent relative frequency of different types of behaviour but would not bias the results on the relative sociability of individuals unless some individuals engaged more frequently than others in the more noticeable activities. Chalmers (1968a) attempted to correct for this bias by measuring the ratio of exposed: partially concealed animals performing different activities. Aldrich-Blake (1970) however, concluded that the correction was not of value unless it could be shown that the ratio of seen: unseen was the same as exposed: partially concealed. In the Ain Kahla habitat where there was little undergrowth and, by the nature of cedar trees, an open canopy, this bias will be less important than in dense tropical forests. Some sessions included periods when the animals were on the slopes and observation was easy. I have not used a correction factor.
(ii) Some animals may be seen less frequently than others either because they were less habituated or less attached to the group and hence more frequently out of the observer's sight. In retrospect I should have investigated this possibility by recording at fixed intervals the identity of all those visible. At the time this was not done simply because there was usually no indication that some individuals avoided the observer. Exceptions to this included a mother with a recently born baby who was more nervous of the observer and vigilant males who were more likely to be visible. These were both temporary states, vigilance behaviour for instance, soon declined and was usually not seen (fig. 7.2). During the non-mating season there was no evidence to show that some animals were less attached to the group; movements away from the group were rare (section 4.2.1). This state was emphasized to me at the end of the project when suddenly some adult males and females became less obvious and I found that they were copulating away from the group. Since I shall be concentrating here on the non-mating season this will not affect the results (section 9.2.3). The possibility of this bias was also reduced by the observer moving around the group and not just observing from one position.

(iii) At first some individuals (chiefly juveniles and infants) could not be recognized or were recognized with difficulty. To prevent these individuals from being under scored I excluded from the analysis the first 479 social interactions. After that I was confident of recognizing all individuals. The results presented in chapter 14 show that some individuals participated in relatively few social interactions and it might be thought that these individuals were being under scored. In fact the two animals that appeared least frequently (AF5 and AF6) were two of the most easily recognizable animals.

(iv) On rare occasions the flow of behaviour was so great that the observer was swamped with data. This happened when there were large scale fights involving most of the group or when several complex interactions were in view at once. In these cases I attempted to record as much as possible. I intentionally made no attempt to record play in terms of its components and this considerably reduced the complexity of the data.
BM2 was not born until ca 23.6.69. It therefore missed the first 279 interactions (12.44 hours of data) and during that time its mother AF4 was theoretically a subadult. To avoid complications AF4 was treated as adult throughout the single group study and no correction has been introduced for BM2. In many cases therefore the scores for this animal should be higher than those given.

One of the reasons for introducing the nearest neighbour study was to provide an independent check on the behavioural observations. The nearest neighbour study used very different methods (section 13.2) that eliminated biases (ii), (iii), (iv) and (v). (i) may still have been operating since the method assumed that when recorded the animals were in their typical positions relative to other animals. Apart from this it is unlikely that a logical correspondence between the results of the interaction and nearest neighbour methods is due to them being biased in the same fashion. (See also p 431.)

9.2.3. The data sample analysed.

Details of continuous recording sessions are given in table 9.1. For the reasons outlined above the first 479 interactions were discarded. Of the remainder, 973 were recorded during the mating season and since that involved a considerable change in behaviour the following analysis is restricted (unless otherwise stated) to 1740 interactions recorded in the non-mating season. Data on the general characteristics of these interactions are given in chapter 14. For the present it should be noted that continuous recording sessions were spread throughout the daylight hours (fig. 9.1). Only where specifically noted were the results corrected for the unevenness in the distribution of the sessions. The sample represents a variable proportion of the interactions proceeding at any one time and for this reason comparisons of the frequency of events must be restricted to their relative frequencies. No measurements were made of the absolute frequency of events.

9.2.4. Defining a social interaction.

One of the most striking aspects of primate groups is their social nature with an almost constant flow of behaviour. Closer
FIGURE 9.1. The diurnal distribution of continuous recording sessions for the data sample analysed.
examination however shows that an individual does not interact continuously with its companions; bouts of social behaviour are interspaced with feeding, resting, or other non-social activities. The strongest argument therefore in favour of splitting up the flow of behaviour into social 'interactions' is that the animals themselves appear to do this. A social interaction is defined here as a continuous bout of continuous social behaviour between two or more individuals. Interactions varied in their length and complexity; a brief interaction might simply involve two individuals glancing at each other. A lengthy agonistic sequence involving a variety of animals at different intervals is obviously more complex. An interaction was greater than the animals involved in it; initial participants frequently left before the end. Interruptions in visibility meant that many interactions were only partially observed and consequently the flow of behaviour appeared to be even more disjointed than it actually was. The termination of an interaction was scored when there was a break in communication and association between the animals. This conveniently included in social interactions many animals that had ceased actively signalling but had remained either behaviourally or spatially orientated towards the other members of the interaction.

When dividing behaviour into social interactions the occasional difficulty arose and some assumptions had to be made. One interaction is never independent of other interactions occurring at the same time or shortly before and after the interaction in question. Any interaction must, at least indirectly, influence another by simply excluding the possibility that an animal could simultaneously participate in two interactions. At present this limitation is best ignored. Secondly there is the problem of actually dividing the observed behaviour into interactions. This was most acute when the period of non-social behaviour between two 'interactions' was brief or when two 'interactions' were related. Consider the following examples:
(i) A grooms B; D chases C that screams; B runs from A and joins D in chasing C.
(ii) A grooms B; D chases C that screams; C runs to A and B and also grooms B. D is no longer involved.
(iii) A threatens B which moves from A and then threatens C which presents to B.
(iv) A threatens B which presents to A and threatens C.

In the first three cases two separate interactions would be recorded. (iv) would be recorded as a single interaction since B continued to communicate with A while also communicating with C. In examples (ii) and (iii) the separate interactions were related to each other and in the analysis the occurrence of such cases was specifically noted.

A third problem was the difficulty of handling interactions that merged. Consider for instance:

A plays with B  C plays with D

A B C D play with each other.

In most cases a brief pause of communication between the participants in one interaction preceded the merging of interactions. In cases where this did not occur it was arbitrarily decided to stop the interaction for which least detail was available (or the shortest) at the point where merging occurred. The splitting of an interaction into two was usually easier to handle.

A fourth problem arose owing to the special position of babies during the early weeks of life. Because babies were removed from their mothers in the first week of life (Section 11.4) the mother-baby pair could not be considered as a constant unit which could be treated as one individual and not two. It was essential in this respect to place equal weight on all individuals. Babies did not, however, move about freely on their own until about 9 weeks old. By my definition of an interaction, young babies would therefore be involved in one long social interaction. As a consequence all sightings of a baby would be recorded as incomplete with an unknown
start and finish since the baby was always with another animal when it came into view or was lost from sight. The following procedure was adopted with babies from birth to ca 9 weeks old (i.e. before 21.7.69 for BF1; and 30.8.69 for BM2).

Each sighting of an animal with a baby was recorded as a separate interaction irrespective of the actual ongoing behaviour between the monkey and baby. If the baby was with only one animal when it came into view or was lost from sight, then that part of the interaction was recorded as complete; otherwise breaks in observation were recorded as appropriate. If others became involved with a monkey with a baby, then the flow of behaviour was split into separate interactions just as if the baby was not there. If a monkey with a baby left an interaction in progress (and ceased to interact with others in the interaction) then this was recorded as the start of a new interaction between the monkey and the baby. Examples of this approach are given in fig. 9.2.

After ca 9 weeks of age this approach was continued except that a break of observation was recorded if the monkey-baby pair came into sight or were lost from sight together. This therefore did not affect the overall proportion of interactions the babies were scored in. One reason for selecting this whole approach was that it would not inflate or underestimate the natural division of the behaviour of older animals into social interactions which were usually quite distinct irrespective of the presence of a baby.

9.2.5. Behaviour recorded.

In addition to, or instead of, the behaviour patterns given in Section 8.2 the following constellations of patterns were recorded.

**Passive avoidance.** Defined in Section 10.2.2. Move to or move near preceding this pattern were not scored unless passive avoidance was preceded by the subject giving some other behaviour (e.g. present).

**Threaten.** Defined in Section 10.1.2. Specific patterns (e.g. facial expressions) were recorded whenever possible.

**Active avoidance.** Defined in Section 10.4.
FIGURE 9.2. Example of the division of social behaviour sequences involving babies, into separate social interactions. The examples (i) to (iii) should be read from left to right.

Key. A, B, C etc. = monkeys; b = baby; CIS = comes into sight; LFS = lost from sight. Solid line = interaction in progress between one monkey and baby; dashed line = interaction in progress with more than one monkey and baby; dot-dash line = interaction without baby. Curved arrows show monkeys joining or leaving interactions. (1), (2), (3) between vertical markers are social interactions defined as distinct using the criteria noted in the text.

With babies older than 9 weeks a break in observation (e.g. start/finish of interaction not seen) was recorded where CIS and LFS are marked. When less than 9 weeks old this was not recorded, each sighting being recorded as complete when the baby was with only one other monkey at that time (see text).
The above were qualified by the context whenever possible and appropriate. Contexts scored were, proximity, food position, water position, grooming position, from the presence or interaction with a third monkey (excluded grooming position) and as dyadic threats from a distance. They were also qualified to state whether or not the action was dyadic or greater than dyadic. (The meaning of these terms is explained in chapter 10.)

Friendly approach. An approach by the subject without threat which did not give rise to retreat (or the patterns associated with retreat or submission) by the object. The object on some occasions threatened the subject. 'Non-friendly' approaches were not recorded as such but under the threat system. Friendly approach and follow were mutually exclusive.

Leave. A monkey moved away from the animals with which it had been interacting or terminated its part in an interaction in some other way - for instance, by turning and feeding. This pattern excluded any form of flight or avoidance. A baby or infant being carried by a monkey that left a social interaction, was not itself recorded as leaving.

Look at. For the purposes of quantification this was only included when it was not given in association with another behaviour pattern.

In contact. Quantification was considerably simplified by ignoring all except the most obvious and lengthy instances of in contact.

Play. Was generally scored in terms of combinations and not permutations of playing individuals. Order was only considered when one animal initiated play.

Pay attention to. Subject(s) bent over a baby or infant in such a fashion that the details of their interaction with the object could not be more accurately scored. Mouth baby/place face close to baby in unspecified way was also recorded.
End grooming. The subject, either groomer or groomee, terminated an allogrooming bout. This is discussed in more detail in chapter 3 where details of the qualifications used to record context and the timing of allogrooming bouts are given.

Run to. Subject ran towards a fight it had previously not been involved in. This did not specify in any way the action of the subject after approaching the fight.

Subject with a baby/object with a baby. Used to define cases in which the subject or object was with a baby. The definition used varied with context. (i) In the case of friendly approach or leave any animal which at that instant was in the same interaction as the baby and being simultaneously approached or left, was recorded as object with a baby. (ii) In all other cases e.g. a subject with a baby making a friendly approach, leaving or performing any other pattern or an object having any other pattern directed at it, was recorded as subject/object with a baby only when it was actually in contact with the baby (i.e. in contact in a general sense and not as defined in pattern 52). The identity of specific babies was recorded.

Finishes previous behaviour was not specifically recorded except in special cases such as grooming (see above).

A key problem with a study of this sort is knowing whether all behaviour patterns were being scored with equal efficiency (Altmann 1965). This is especially true with the more obscure patterns which might easily be ignored in preference to the more obvious ones. Since there was only myself observing it was not possible to get an independent check on this. It was recognized, however, that certain patterns were being under scored. These patterns (including several orientation postures, contact, ignore, avoid, end grooming, leave, look at and cradle) were coded into the data but excluded in some specific searches, for instance, when examining the relative sociability of individuals (chapter 14). *See page 214.
An additional problem was to be sure that the level of description used was relatively uniform throughout the period of data collection and for different types of interaction. Considerable experience in recording protocols had been gained during the population study and the rejection of the first 479 interactions (Section 9.2.2) resulted in the exclusion of interactions recorded before the technique had stabilized. Details of the level of description used are illustrated by examples of the data in fig. 9.3. Apart from the inclusion of some of the constellations of patterns listed above, it corresponds closely to the level of description used by Altmann (1962, 1965, 1968).

9.3. TECHNIQUES OF ANALYSIS.

Social interactions were coded and fed into a Digital Line 8 computer where the relevant searches were made. The system used, a general one for ethological data, was developed by D. Vowles and J. Clark and more recently by C. Holmes. C. Holmes modified and developed new programs specifically for this analysis. Results on the interactions between individuals were obtained in the form of matrices which were manipulated and interpreted on an I.C.L. 4-75 computer using programs written by the author.

For each interaction two types of data were prepared, both in a verbal format. The following is an outline of the major features.

(i) 'E-data' or data on the background to the social interaction. This included:

The interaction code number.
The date.
The time in 15 minute periods.
Whether the record of the interaction was complete and if not whether the breaks came at the start, middle or end.
The types of behaviour included (7 categories discussed in chapter 14).
Whether grooming was included and if so whether the duration was known.
The sex, age-sex class and identity of the participants. Where there was incomplete information this was coded in as much detail as possible.
The number of animals participating in the interaction.
Example 1. Protocol.
BF1 runs to AF2 and is lost from my sight against AF2's chest.
SF1 approaches AF2 and BF1 and sits with her arm around AF2.
AF2 threatens SF1 away. (1. Sept.'69, 14:40 h).

E data
319  SEPT 1ST- 11-- 0300
AGON MATE AQEA COMP
FEMA ADFL QFEM SUBA QFEM BABY QFEM U3--
M13- M16- M24-.

B data
319
1  SM24 FA-- OM13.
2  SM24 VVen OM13.
3  SM16 FA-- OM13 OW24.
4  SM16 FA-- OK24.
5  SM16 TITC SIDE OM13 OW24.
6  SM16 ARMQ OM13 OW24.
7  SM13 SW24 THRE PROX FMOD OM16.

Example 2. Protocol.
SM1 threatens JM3 over proximity. This sits facing him giving a low-intensity lip-smack face, but SM1 keeps threatening and the juvenile's expression changes into a teeth-chatter face. SM1 threatens it again, then teeth-chatters and presents to JM3 and turns away from it. (1. Sept. '69, shortly after 1456 h.)

E data
378  SEPT 1ST- 14-- 0045
AGON COMP
MALE SUBA QMAL JUVE QMAL U2--
M5-- M8--.

B data
378
1  SN5- THRE PROX FMOD OM8-.
2  SM8- LSP- OM5-.
3  SN5- THRE PROX FMOD OM8-.
4  SM8- TCF- OM5-.
5  SN5- THRE PROX FMOD OM8-.
6  SM5- TCF- PRES OM8-.
7  SM5- LEAV OM8- . 0

BM2 is alone in a tree and screaming ...... JM2 runs to the tree and climbs up to it. He picks it up, holds it to his chest and teeth-chatters to it vigorously (1741). The baby changes its calling to chups. JF2 climbs up and joins them (1741½) and bends down teeth-chattering towards BM2's face. She starts to groom JM2. While BM2 is cradled in JM2's lap it gives occasional chups and cheeps. At 1748 the baby climbs onto JM2's shoulders while he is being groomed. JM2 looks up at it, teeth-chatters vigorously and gets up (BM2 having clung onto his back) so terminating the grooming. He moves carrying BM2 to the next tree and is lost from sight. (27. Aug.'69).

E data

234 AUGU 27TH 17-- 0300
APEA COMP ALEN GROO
MALE FEMA JUVE QMAL QFEM BABY QMAL U3--
M7-- M18-- M25--.

B data

234
1 SM25 DISS.
2 SM7- FA-- OM25.
3 SM7- VEMB OM25.
4 SM7- CRAD OM25.
5 SM7- TCP-- OM25.
6 SM25 BABB CHIP OM7--.
7 SM18 FA-- OM7-- OW25.
8 SM18 FA-- OM25.
9 SM18 SITC OM7-- OW25.
10 SM18 TCP-- OM25.
11 SM18 GROO OM7-- OW25.
12 SM25 SIST OM7--.
13 SM7- TCP-- OM25.
14 SM7- CARR OM25.
14 SM7- SW25 ENDG GELE LEAV OM18.0
An example of E-data is given in Fig. 9.3. This data was used for two purposes: either to search for the frequency of events or combinations of events coded in the E-data (e.g., the number of grooming interactions at a certain time of the day) or to search for specific interactions (e.g., all those involving adult males) and then to hold these for specific searches of the corresponding B-data.

(ii) B-data or data giving the sequence of behaviour in a social interaction.

Each interaction was numbered to correspond to the relevant E-data and each line of this data (see Fig. 9.3), in the typical state, included a specification of:

The subject - the individual (identified as accurately as possible in terms of its individual name, or failing that age and/or sex if known) which made the behaviour pattern(s).

The verb(s) one or more of the behaviour patterns specified in Sections 8.2 or 9.2.5.

In some cases a qualifier to the verb giving additional specific information (e.g., in the case of passive avoidance whether this occurred over proximity or a water position).

The object - the individual to which the behaviour pattern was directed.

Lines included an event number. All lines with the same number referred to behaviour that happened simultaneously, and the sequence of event numbers corresponded to the sequence of events in the interaction.

The format of this data was semi-flexible, for instance, objects could be omitted if required. Breaks in observation were also coded. The system deals with the order of events and not the time separating them. B-data was used for two main types of searches either on a complete data tape or on specific subsets of data preselected by E-data searches. Searches for individual verbs or subject-verb-object combinations gave information on the frequency of specific behaviour patterns and the frequency with which individuals gave (or received) patterns to (or from) other individuals. More
complex searches permitted the examination of transitions either between lines with the same event number or between lines with consecutive event numbers. The data was carefully coded and searched so that all transitions were based on either inter-individual or intra-individual transitions (as required) and never a mixture of the two.

The reader will be aware that the above techniques of analysis are potentially more powerful and sophisticated than the method of data collection. For this reason the examination of transitions, for instance, was kept to a minimum and used only to answer specific questions. No overall matrix of transitions was produced. The technique assumes that patterns commence in a chain-like sequence and, although it records when patterns or events occurred simultaneously, it does not cover cases in which patterns started sequentially but continued simultaneously. The data collection method, based on only one examination of the interactions and not the repeated examination of video-recordings or film, will tend to overemphasize the simultaneous occurrence of patterns.

9.4. SUMMARY.

The methods used to sample the distribution of social behaviour between the 25 individuals in one group of monkeys are discussed. The technique involved recording all of the social behaviour visible to the observer during timed observations sessions (continuous recording sessions). This method was selected in preference to following the behaviour of one individual at a time because it focused on social interactions and the flow of behaviour between individuals, rather than intra-individual behaviour. A social interaction was defined as a continuous bout of continuous social behaviour between two or more individuals. 3492 interactions were collected at a mean rate of one every 2.7 minutes and the analysis presented in subsequent chapters is based on 1740 of these (spread throughout the daylight hours) from the non-mating season. It is recognized that there are several potential sources of bias in
the data collection technique and these are discussed. The data was examined using a computer programmed to permit analysis in terms of the frequency of events (or combinations of events), the frequency of behaviour patterns being used between individuals, and transitions of behaviour between and within individuals.