ECOLOGY AND BEHAVIOUR OF THE VERVET MONKEY
CERCOPITHECUS AETHIOPS PYGERYTHRUS
LOLUI ISLAND, LAKE VICTORIA, UGANDA.

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MEMORANDUM

The design and execution of the studies on which this dissertation is based are the sole and unaided work of the candidate, unless otherwise indicated and acknowledged in the text.

CONTENTS

Vegetation

INTRODUCTION

INTRODUCTION

The field study of primate social organisation and behaviour has expanded rapidly during the last decade. Indeed, prior to the early 1950's the only systematic field studies were those of Nissen (1931), Bingham, (1932) and Carpenter (1934, 1940, etc.). During the 1950's studies were begun on baboons, Papio spp. in Africa, (Bolwig, 1959; Hall, 1960; Washburn and DeVore, 1961), and on macaques, Macaca spp. in India, (Prakash, 1958; Nolte, 1955 a,b.). All these studies were the result of an interest in primate behaviour originating chiefly in their early use as laboratory animals, primarily in the field of comparative psychology (Kohler, 1925; Yerkes and Yerkes, 1929). An apparent exception were the field studies of the Japanese macaque, M.fuscata, begun during the 1940's but which did not become known outside Japan until much later (Frisch, 1959).

Comparative psychology, although concentrating on differences between different species of animals, was chiefly concerned with the comparison of mental processes and the phenomena of learning, and not directly with problems of social organisation and behaviour. These latter questions were not generally even considered as important problems. Eventually, when attempts were made to construct theories explaining primate congregations and their structure, it was perhaps inevitable that they were based on mentalistic theories of proximate causation and only loosely related to selection theory and evolution.

Theories important in influencing later field studies were derived exclusively from studies of captive and caged animals. The question of the adaptive significance of social structure and behaviour was unlikely to receive a satisfactory answer from studies of groups which were maintained as units by the presence of walls, wire or bars, and in which the normal patterns of maintenance behaviour were grossly distorted. The problem of the adaptive significance of different patterns of social behaviour is likely to arise in the first instance in an attempt to fit observed variations into meaningful perspective. One of the reasons permitting the construction of over-simplified theories of social organisation was the observation that, under captive conditions, a certain similarity and rigidity of social behaviour in different primate species and genera obtained.

The two main motivational theories which have influenced all subsequent field and laboratory studies of primates are, respectively, the theory of the "sexual bond" as the basis of primate congregation, and secondly the theory of "social dominance" which was put forward to explain the structure of the congregations. The theory of the "sexual bond" was first put forward by Zuckerman (1932) and relied heavily in its theoretical orientation on the works of the psychoanalyst Kempf (1917). The theory of "social dominance" cannot be attributed to any one worker, but several of the most important influences on the development of the theory and its use in primate behaviour studies were the writings of William McDougall (1908), T. Schjelderup-Ebbe (1931) and A.H. Maslow (1936).

The theory of the "sexual bond" as the motivational basis of primate congregations had at least the merit of being explicit and capable of being stated in terms which made it subject to empirical proof or disproof. Most field studies have consequently attempted to obtain data on the periodicity of mating and the presence or absence of birth seasons as a critical test of the theory. The data available up to 1965 was summarised by Lancaster and Lee (1965) who concluded that constant sexual attraction could not be the basis for the persistent social groupings of primates. These authors further claim that where copulation is restricted to a few months during the year, as in some macaques, no variations in the strength of the social bond are observed.

The theory of the "sexual bond", having, now been subject to critical analysis in the light of a considerable body of data, requires very little further discussion. The influence of the theory on field studies has been considerable, but at least it has been overt, and the data collected with explicit reference to the theory. This has not been the case with the concept of "social dominance" which has probably had even more influence on the design and interpretation of field studies, and which even today still exerts a powerful influence within this field.

"Social dominance" has been used as both a descriptive and an explanatory concept and with many different shades of meaning, with the result that even today there is considerable ambiguity as to which precise behaviour patterns any given use of the term refers. It seems important, therefore, in a study of the relationship between social behaviour and the environment, to examine the validity of one of the basic concepts which is fundamentally mentalistic and proximate, and which was derived from studies of groups living in highly artificial conditions.

The use of the concept in comparative psychology owed a great deal to McDougall's theory of social instincts. McDougall, (1908) considered that the characteristic of "instinctive" behaviour was that it was a "purposive striving". There was then a tendency for every instance of behaviour considered both purposive and striving to be ascribed a specific instinct. McDougall considered also that every instance of instinctive behaviour involved both a <u>knowing</u> of an object, a <u>feeling</u> in regard to it and a <u>striving</u> towards or away from it. The mentalistic formulation of this statement in terms of "knowing" rather of "perception" permitted the postulation of intervening intellectual functions such as "judgement", and gave rise to a tendency observed in workers such as Yerkes (1929, 1939) and Maslow (loc. cit.) to consider an animal capable of choosing whether or not to assert its "social dominance" which was still, however, considered to be an instinct.

Generalisations from studies of captive primates

The development of the theory of "social dominance" as the normal structuring mechanism of primate societies was permitted, as has been pointed out, by observations of similar rigidities in social behaviour in different primate species such as the chimpanzee, the macaque and the hamadryas baboon. There is considerable internal evidence from these early studies indicating that the populations studied were under severe social stress. Zuckerman

(1932) gives a list of the common diseases causing death in his captive colony, and the number of deaths from fights, both of which are indicative of a severely pathological social condition. Carpenter (1942) gives details of the high mortality rate of the rhesus monkey group following its importation onto Cayo Santiago island to live in conditions supposedly similar to the natural habitat. Chance (1956) gives details of the high incidence of disease in the colony of macaques of which he studied the social structure. It seems likely that the increase in aggression noted under captive conditions and the increased susceptibility to disease indicate an attempt to regulate the numbers of the population to those appropriate to the restricted ecological conditions of captivity. Christian (1963) provides evidence that density dependent positive pituitary-adrenal and negative pituitary-adrenal responses might regulate the growth and decline of populations by inhibiting reproduction, enhancing susceptibility to disease, and it does not seem unreasonable to assume that this adjustment is common in captive primate populations.

There is field evidence that the type of social structure most efficient under ecologically impoverished conditions, or where there are seasonal food shortages is the one-male-group system, described by Kummer and Kurt (1965) in Papio hamadryas, Hall (1966) in Erythrocebus patas, and Crook (1966) in Theropithecus gelada. All these species, it should be noted being animals of the arid regions of Ethiopia and the Sudan. These different genera are also not closely related, any similarities in the social structure must be concluded to have arisen from convergent evolution. Under the impoverished conditions inhabited by these three species there has thus been adjustment to the one-male-group system. This means that animals not directly concerned with the rearing of infants are excluded from the social group. The pathological behaviour exhibited in captivity and which permitted the construction of the "social dominance" hypothesis as a descriptive and explanatory concept may therefore be an example of the process of adjustment only exhibited under conditions of severe deprivation, and only indirectly related to the structure and behaviour of groups under adequate environmental conditions.

Conclusions about the "normality" of "social dominance" as a social structuring mechanism were also permitted by many experiments which were faulty in design, experimental criteria and logical consistency. In Maslow's investigation (1936) for example, groups in which comparative levels of "dominance" were assessed consisted of different genera and age-sex classes of primates, and including in one case a Coati, Nasua sp. The same criticism applies to the investigation by Maslow and Flanzbaum (1936) where the animals were housed individually and tested in pairs which were "equated for weight, sex, age and usually* species." Warden and Galt (1943) admitted species differences in the manner in which the "hierarchy" was organised, rhesus monkeys, for example being organised by "fighting and biting". Cebus monkeys, on the other hand, organised their social structure by "vocal combat only". Yet these authors made the

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*my underline

different species compete with one another and concluded that the motivating factor "social dominance" was responsible for both "hierarchies" and was therefore less strong in one of them.

It is clear, therefore that workers going out into the field for the first time, equipped only with concepts derived from captive studies, were probably expecting to find broad similarities between species similar to those found in captive conditions, and a social system based on the principle of "social dominance".

The concept had not, however, been completely adequate to explain even the structure of captive groups. Yerkes (1943) for example stated that an "obvious defect" in the working of the "dominance principle" was the possibility of abuse. Among chimpanzees, said Yerkes, there are "bullies and racketeers" ready to take advantage of their social position to impose themselves upon an individual or group. Cruelty and injustice, said Yerkes, inevitably results. This statement emphasises the extent to which the postulation of mentalistic intervening variables had become possible at this time.

The ambiguity resulting from the undefined nexus of "instincts", "drives" and "judgement" was increased by the lack of frequency with which the concept was defined. Definitions were often made in terms of the probability of access to the appropriate drives of interacting individuals (c.f. Carpenter, 1954) and are often circular. The incipient difficulties experienced in the application of the concept to wild populations were also beginning to become apparent. Chance (1956) says that dominance is usually defined as priority of access to a need satisfying object, but he goes on to state that in the particular group in question "no priority of feeding was shown", and concluded that "it was in the relations of the animals to each other that the order of rank was made manifest."

These examples emphasise the reliance which was placed on the concept both as a descriptive and an explanatory concept at the time when the field study of primate behaviour was beginning to expand.

It should also be emphasised that only in the study of primate behaviour was the concept of a "social hierarchy" considered to be a characteristic of the population, rather than an interpretation of the reliability of dyadic interactions seen by the observer. Allee (1938), for instance, noted that irregularities and triangular relationships were by no means uncommon, even in established flocks of birds. A hen which is otherwise the alpha bird in the pen may be pecked with impunity by some low-ranking member, said Allee, although the latter is in turn pecked by many birds over which the alpha hen has a clearly established social superiority. This inconsistency Allee considered to be a result of the fact of the low-ranking bird having first met the alpha bird on one of the latter's "off days", gained an advantage in the first combat and managed to keep it thereafter with the aid of the "psychological dominance" thus established.

The position taken by Allee and many ornithologists contrasts strongly with the position commonly encountered in primatology, where the hierarchy has been considered to be the structural element of the group and not an abstraction on the part of the observer.

There is considerable evidence from both field and captive studies of primates to indicate that the position in primates is not disimilar from that recorded by Allee in flocks of domestic hens. Thus Itani (quoted by Altmann, 1962) states that

> " The rules of hierarchy do not seem to be kept so well by the subdominant males, and they often* take a tangerine to which one of the dominant males has a right. It would seem that they neither know the rules of dominance followed by the dominant males nor do they feel they will be caught. "

It is clear that under crowded captive conditions, where there is a tendency both for aggression to increase and for disease to be common, the outcome of dyadic interactions becomes predictable. The factors important in this process are probably various, depending on the health, age and sex of animals involved and the nature of the dyadic interaction. There is, however, no evidence indicating that a "hierarchy" is other than an abstraction from the increased reliability of the outcomes of the dyads, nor that there is any unitary motivating "social dominance drive".

"Social dominance" and primate field studies

Field studies on primate species that have been studied previously only in captive conditions provide some control in demonstrating the differences in social structure and behaviour under captive and wild conditions.

Kummer and Kurt (1963) in a careful study of *Papio hamadryas*

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*my underline

concluded that it was possible, although not likely, that a dominance hierarchy might operate amongst wild P. hamadryas males. In several months of study they failed to find either a dominance hierarchy or any males who were dominant over all the others. They admit that this may be due to the difficulty in analysing the problem in the large sleeping-parties and of the rare social contact between adult males. They consider, however, that hierarchies are unlikely to develop in open parties that frequently change their composition.

Van Lawick's studies of wild chimpanzees (1963, 1965) have also failed to find a social structure and behaviour that might have been expected from Yerkes' detailed studies on the dominance relations of the species. Aggressive and submissive interactions were infrequent, and the concept of a hierarchy could not be substantiated within the temporary groupings.

Other field studies have demonstrated a variability in social structure and social behaviour within single species that could not have been either expected or predicted from the proximate mentalistic theories of social organisation. Thus Jay (pers. comm.) has discovered wide variations in group size and social behaviour in M. mulatta which are apparently correlated with habitat differences. Jay (1963), and Sugiyama (1965) have also described very different social systems within the same species, Presbytis entellus.

The differences described thus far are variations in observed behaviour other than would have been expected or predicted from studies of captive groups. But the "social dominance" model derived from these original studies has continued to be used to describe the structure of wild-living groups, and has met with varying degrees of success.

Kummer (1957) having failed to detect a classical hierarchical organisation in P.hamadryas pointed out that the ranking of individuals into a hierarchy assumes an underlying continuum of rank-order criteria. This was not applicable to his wild groups, and in captive ones was of value only in limited age, sex and behaviour categories. Aggressive behaviour, for example, he considered to be a good indicator of rank in adult females, although it did not differentiate two and three year olds, and was completely inapplicable in one year olds.

DeVore (1965) also found the classical hierarchical concept inadequate to describe the structure of Papio anubis. He points out that in any troop containing three or more adult males, the dyadic relationship between any two males was very rarely independent of the relationship between each member of the dyad and other males in the troop. Even more important, says DeVore, certain adult males constantly associated with each other in groups of two or three and tended to aid and co-operate with each other during aggressive interactions with other males. DeVore established the concept of a "central hierarchy" to explain the structuring of these groups, and pointed out that very low ranking animals, individually considered, were sometimes very high in terms of membership of the "central hierarchy".

The classical concept of "social dominance" as the normal means of structuring primate societies seems therefore to be inadequate in view of the observed variability of primate social structure under natural conditions. A theory of proximate mentalistically conceived causation would not have predicted these differences which seem ultimately to be related to selection pressures determining efficient dispersal of the population through the environment.

Recent attempts have been made to explain the observed variability of primate social organisation, which, as has been pointed out, is sometimes considerable even within a given species, in terms of selection pressures and evolution. (c.f. Crook and Gartlan, 1966). These authors conclude that the social structure of any primate population depends on characteristics of the environment such as food availability and dispersion, the type and availability of sleeping sites, and predation pressures interacting with features of the population such as size, dispersion, mating patterns and learning processes. Any species which is anatomically specialised and restricted to a narrow ecological niche may therefore be expected to have a rather stereotyped and restricted social system.

Many of the primates commonly used in laboratory studies and on which the early captive work was carried out, such as the macaque, are not specialised for a narrow ecological niche, but for life in a variable environment such as the savanna. This applies also to Cercopithecus aethiops. These species seem capable of social adjustment to the particular conditions of the environment in which they are living. With a geographical distribution as widespread as that of M.mulatta or C.aethiops it is to be expected that variations in habitat types in different parts of the range will be observed and this is found to be the case. Under conditions of severe ecological impoverishment, comparable but less extreme than the conditions normally encountered in captivity, it is to be expected that the adjustment process will tend to produce the one-male-group system which has been evolved independently in those terrestrial species living around the perimeter of the Sahara. There is field evidence of differences in the sex ratio of groups nearer the extremes of the distribution range which the hypothesis would predict, both for C.aethiops and M.mulatta. In captive conditions, therefore, adjustment would involve not only reductions in the total number of animals, but also particularly the elimination of surplus adult males.

Any field study concentrating on the social structure of the population, especially those geographically widespread species mentioned, should therefore describe the relationship of the population with the entire ecosystem. It is only in these terms that many of the social patterns become explicable, and observed differences meaningful.

The basic orientation of this study can therefore be described as relating the social structure of the population to those aspects of the environment which form major selection pressures. It was found necessary in this study to pay more attention to the structure of the ecosystem than has generally been the case in previous studies.

A second main object was to avoid, as far as possible, the description of the social structure of the population in terms of a model which carries with it implicit and unjustified motivational overtones, which is inadequate to deal with variability and complexity, which leads to distortions in both the collection and interpretation of data, and which is only in the loosest sense compatible with theories of selection pressures and evolution. The social structure was described, as far as possible in terms of observed interactions and of social roles which were apparently important in the integration and success of the group in the particular environment of Lolui Island.

Literature

The majority of the literature on the C.aethiops species group consists of incidental reports by occasional travellers and adventurers, generally relating to West or South Africa. These reports are generally unsystematic and anthropomorphic in nature, and occasional whimsical. The most that it is generally possible to glean from these sources is an indication of habitat type, population density and some of the basic agonistic behaviour patterns.

This lack of information about even the most basic facts of the distribution and social behaviour of the species was inevitable in view of the lack of knowledge of the African continent itself, most contact being for the purposes of trade and not penetrating far inland. Even by the end of the nineteenth century, when the Victorian explorers had opened up the continent, knowledge of the species was still fragmentary.

Many of these early reports stressed the complete arboreality of the species, a fact which emphasises the ease with which the species uses trees. From the Lolui data it became clear that animals would remain on the ground in the presence of a human observer only after a period of habituation. In the National Parks of East Africa, where animals are protected from human interference, the more normal patterns of time spent on the ground and in the trees is generally seen.

Buffon (1886) records them as crop raiders and also gives information about the social vigilance behaviour and alarm behaviour of the species in the following terms, "l'un d'eux fait sentinelle sur un arbe, pendant que les autres se chargent du butin; s'il aperçoit quelqu'un, il crie houp, houp, houp, d'une voix claire et distincte; au moment de l'avis tous jettent les cannes (sugar canes) qu'ils tenaient dans la main gauche, et ils s' enfuient en courant à trois pieds."

The description of this call and the manner of escape suggest, in the light of the Lolui information, that the group concerned was not really frightened and was probably used to being chased from the crop.

Twentieth century literature on the species has been largely concerned with problems of taxonomy. Often the species is only mentioned incidentally in the course of natural history accounts, or during studies of other species. Haddow (1952) for example gives a silhouette diagram for the recognition of the species in forest conditions but does not otherwise mention it.

Starck and Frick (1958) were the first workers to study the species in systematic detail, but only as part of a programme on the primates of Ethiopia. They give information about the breeding biology, social behaviour, day ranging patterns and postures of the species.

Since this study several workers have undertaken studies of the species group in different parts of Africa. C.K. Brain (1965) has studied the species in both wild and captive conditions in Rhodesia and South Africa. T. Struhsaker also carried out a study of the species in the Masai Amboseli Reserve which was contemporary with the study reported here.

Morphology and taxonomy

The classification of this particular primate species is one of the more confused areas of primate taxonomy. There are many reasons for this, one of the main ones being an ambiguous description by Linnaeus (1758) of a species he called Simia aethiops. This species was a "monkey with an untufted tail, the crown of the head with erect hairs and upright white hairs on the brow. Body the size of a Diana monkey, dark with the underparts white. Tail covered with fur, underneath rust coloured. Eyebrows crescent shaped, white, oblique. Upper eyelids hairless, white. Ears small and sharp".

In the 13th edition of Systema Naturae (1788) Simia aethiops was referred to specifically as the "Mangabey or White-eyelid Ape". The Green Monkey, or Green Ape, as Linnaeus called it, was called Simia sabaea. This seems to have been the origin of a confusion in generic names which has persisted almost until the beginning of the twentieth century, in spite of the fact that there was a clear description of the genus Cercopithecus by Brünnich in 1772. Martin (1838) for instance in a paper on the cranial features of the mangabey refers to the specimen throughout as Cercopithecus aethiops, the "white-eyed monkey". Jardine (1883) refers to the Green Monkey as Cercocebus sabaeus.

This taxonomic confusion has been exacerbated by the fact that the widely-distributed species group Cercopithecus aethiops is in fact a cline. There appears to have been little opportunity for significant intraspecific differences to develop, although specimens taken from the extremes of the geographical range are clearly distinguishable. The construction of specific or subspecific boundaries is therefore more than usually arbitary in primate classification. Much material was collected by hunters and explorers during the late nineteenth century and the early part of this century by workers such as Ogilby (1841), Sclater (1893), Pocock (1907), and Elliot (1913). Taxonomic divisions at this time were frequently based on very superficial characters that are now known to vary both temporally and with environmental conditions. Many of Elliot's (1913) species and subspecies for this reason cannot now be considered as taxonomically valid.

Dandelot (1959) used, amongst other characters, the scrotum colour of males, the presence of yellow fur in the medial line between anus and scrotum of adult males, and facial characters such as the shape and length of the "sidewhiskers". Several of these characters are now known to be unreliable, such as scrotum colour which changes during maturation and also with the nutritional state and health of the animal, and which has been observed in captivity to change from a bright blue to a pale putty colour over a period of a few weeks (Gartlan and Brain, in press). On Lolui, where there is a minimal possibility of the population being of different subspecies, the presence of the yellow medial fur was variable even within single groups.

Variability in anatomical characters has been observed by Weinbrenn (1930). In a survey of the skulls of South African, Rhodesian and Angolan specimens, she concurred with the view regarding <u>C.aethiops</u> as a single species, and <u>pygerythrus</u> as a subspecies, and concluded that further differentiation into races on the basis of cranial features was not justified in this very widely distributed subspecies (Fig. 1).

In an attempt to assess the reliability of common subspecific assignments, an examination was made of the British Museum collection of skins of male specimens which had been classified as *Cercopithecus pygerythrus pygerythrus*, *C.p.rufoviridis*, and *C.p.johnstoni*, the latter which has been supposed to be the Uganda type. The reference numbers of the specimens are given in Appendix 1.

There were five specimens of *C.p. pygerythrus* in the collection. All had been classified by the collectors as *C.p.pygerythrus*. The skins were examined for five taxonomic characters which show no significant changes with the state of preservation of the specimen. These were firstly, the presence of a black tip to the tail (A), black fur on the feet and ankles (B), black fur on the hands and wrists (C), the red tuft under the base of the tail (D), and sidewhiskers of the shape and form considered by Dandelot to be characteristic of *C.a.pygerythrus*, (E). The results of this analysis are indicated in Table 1, plus and minus signs indicating presence or absence, respectively. These results indicate that only characters A and E were reliable. A similar analysis was carried out of specimens classified as *C.p.rufoviridis*, of which twelve were classified by the collectors as *C.p.rufoviridis*, two as *C.cynosurus* two as *C.whytei* and one as *C.silaceus*. The results are indicated in Table 2.

The type of variation observed in this collection of specimens

Fig. 1

Distribution of Cercopithecus aethiops and of Cercopithecus mitis.

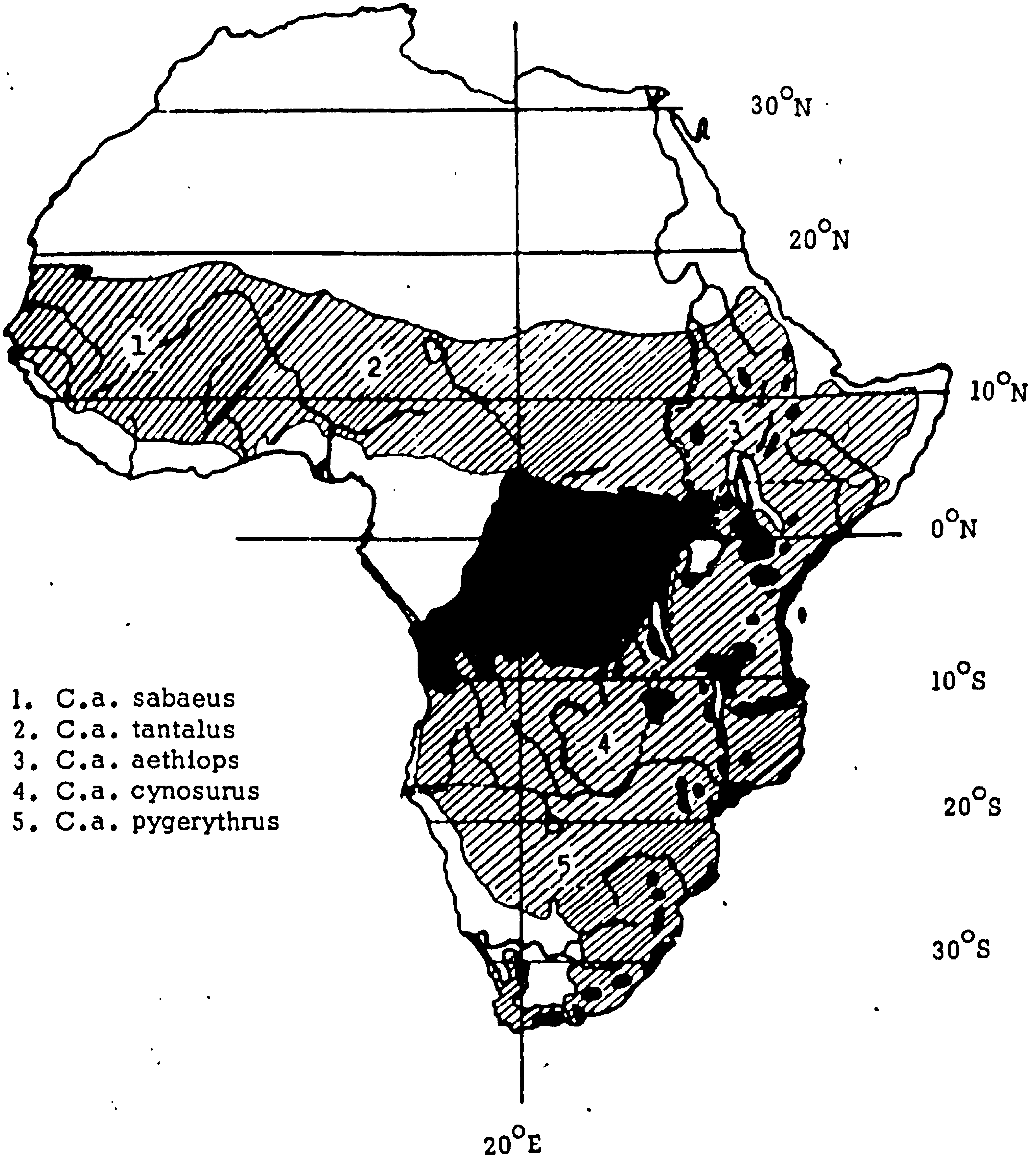


TABLE 1

Presence or absence of characters of supposed taxonomic significance in the British Museum collection of skins of *Cercopithecus pygerythrus pygerythrus*.

Specimen	Character				
	A	B	C	D	E
1	+	+	+	+	+
2	+	-	-	+	+
3	+	+	+	+	+
4	+	-	+	-	+
5	+	n.a	n.a	-	+

n.a. = not available.

TABLE 2

Presence or absence of characters of supposed taxonomic significance in the British Museum collection of skins of *Cercopithecus pygerythrus rufoviridis*.

Specimen	Character				
	A	B	C	D	E
1	+	+	+	+	+
2	n.a	-	+	-	+
3	+	+	+	+	+
4	+	-	-	+	+
5	+	-	-	+	+
6	+	+	+	-	+
7	n.a	+	+	+	+
8	+	+	+	+	+
9	+	-	+	-	+
10	+	-	-	-	+
11	+	-	+	+	+
12	+	-	-	-	+
13	+	?	?	-	+
14	+	-	-	-	+
15	+	+	+	+	+
16	+	+	+	+	+
17	+	n.a	n.a	+	+

is similar to that of C.p.pygerythrus, in that only characters A and E fail to show variation. This point, of course also raises that of the validity of the distinction between the two subspecies.

An analysis was made also of the collection of skins labelled C.p. johnstoni. These were all labelled as such by the collectors. The results are shown in Table 3.

The same type of pattern is again observed in this supposed subspecies, only with two specimens failing to show the characteristic shape and form of the sidewhiskers. There was also an increased tendency for character D, the tuft of red fur under the base of the tail to be absent in this subspecies, only a minority of animals possessing it, compared to a majority in the other two subspecies. This tendency was also observed on Lolui, with the character only appearing rarely in the population.

The data presented on the taxonomic distinctness of the three supposed subspecies indicate a degree of variability within each subspecies and a similarity between them which does not permit the differentiation into subspecies.

In view of present knowledge about the variability of the physical characters previously used as diagnostic indicators, only the main revisions of the genus will be discussed and examples given to illustrate the proliferation of subspecies and races.

In 1893 Sclater published a revision of the genus that included the majority of members. This work was superceded in 1907 by Pocock's monographic classification which arranged the species of the genus into thirteen "groups". Elliot's (1913) classification is

TABLE 3

Presence or absence of characters of supposed taxonomic significance in the British Museum collection of skins of *Cercopithecus pygerythrus johnstoni*.

Specimen	Character				
	A	B	C	D	E
1	+	+	+	-	+
2	+	+	+	-	+
3	+	-	+	-	+
4	+	-	+	-	+
5	+	-	-	-	-
6	+	+	+	-	-
7	+	+	+	+	+
8	+	-	+	+	+
9	+	-	+	-	+

essentially an elaboration of Pocock's 1907 paper, but which raised many of the latter's "groups" to subgeneric status. Schwarz (1928) classified the 159 "forms" then described as belonging to the genus into ten groups, each composed of a number of geographical forms that replace one another locally and are generally connected by intermediate stages. Schwarz's paper is useful as a guide to the affinities of the many different forms described up to that time. Schwarz considered the entire distribution to consist of a single species, Cercopithecus aethiops, with sixteen subspecies. The list of his subspecies and synonyms is given in Table 4.

The aims of binary nomenclature are nullified by proliferations of this nature, and the relations between allopatric but closely related populations are effectively obscured. The classification which was found most useful in this study was that of Dandelot (1959), which is in most respects essentially similar to that proposed by Forbes (1894). Forbes did not utilise the concept of superfamily, which was developed later by Simpson, (1945) but did consider all forms of C. aethiops to belong to a single species group, Cercopitheci chloronoti.

Dandelot (1959), in an attempt to find a term which emphasised both the close relationship and allopatric distribution of the geographically widespread C. aethiops proposed the term superspecies, whereas Forbes preferred species group. The latter term seems to be preferable in that it does not imply a range of variation exceeding that normally observed within a species. This is the case with

TABLE 4

Taxonomy of *Cercopithecus aethiops*, after Schwarz, 1928.

Subspecies	Synonyms
C.a.centralis O. Neumann	*budgetti*, Pocock; *griseisticus*, Elliot; *itimbriensis*, Matschie & Dubois; *benianus*, Lorenz; *graveri*, Lorenz.
C.a.marrensis Thomas & Hinton	
C.a.tantalus Ogilby	*chrysurus*, Blyth; *passargei*, Matschie; *alexandri*, Pocock; *viridis*, A. Schultze.
C.a.sabaeus Linnaeus	*werneri*, I. Geoffroy; *callitrichus* I. Geoffroy
C.a.aethiops Linnaeus	*eugytitthia*, Hermann; *griseoviridis*, Desmarest; *subviridis*, F. Cuvier; *griseus*, F. Cuvier; *cano-viridis*, Gray; *toldti*, Wettstein; *cailliaudi*,

TABLE 4 (continued)

	Wettstein; *weidholzi*, Lorenz.
C.a.hilgerti O. Neumann	*ellenbecki*, O. Neumann; *djamdjamensis*, O. Neumann.
C.a.matschie O. Neumann	
C.a.rufoviridis O. Neumann	*flavidus*, Peters; ?*circumcinctus*, Reichenbach; *whytei*, Pocock.
C.a.johnstoni Pocock	*rubellus*, Elliot; *luteus*, Elliot; *tumbili*, Heller, *contiguus*, Hollister.
C.a.callidus Hollister	
C.a.nesiotes Schwarz	*pembae*, Matschie.
C.a.excubitor Schwarz	*voeltzkowi*, Matschie
C.a.arenarius Heller	

TABLE 4 (continued)

C.a.pygerythrus F. Cuvier	*pusillus*, Desmoulins; *erythropyga* G. Cuvier; *lalandii*, I. Geoffroy.
C.a.helvescens Thomas	
C.a.cynosurus Scopoli	*tephrops*, Bennet; *silaceus*, Elliot; *weynsi*, Matschie & Dubois; *tholloni*, Matschie; *lukonzoolwae*, Matschie; *katangensis*, Lönnberg.

C.aethiops, where the observed variability is much less than in *C.mitis*. For this reason the concept of species group was preferred in this study.

In this study the classificatory scheme of Simpson (1945) was used as far as the generic level. Below this the concept of species group was employed, the actual subspecies being those recognised by Dandelot (1959), although his finer divisions into races were not considered valid for the reasons already given. The classificatory scheme proposed here is not definitive in any sense, detailed anatomical and morphological verification being unavailable, but it is based on geographical distribution and "clusters" of diagnostic characteristics rather than single features. Any merit it may have is therefore in that it takes account of the close relationship of the different forms, and of their widespread distribution throughout Africa, providing at least a systematic scheme for studies of the ecology and behaviour of the entire population.

The details of the classificatory scheme are as follows:-

Order:	Primates, Linnaeus 1758.
Suborder:	Anthropoidea, Mivart 1864.
Superfamily:	Cercopithecoidea, Simpson, 1931.
Family:	Cercopithecidae, Gray 1821.
Subfamily:	Cercopithecinae, Blandford 1888.
Genus:	Cercopithecus, Brünnich 1772.
Species group:	Cercopithecus aethiops, Forbes 1894.
Subspecies:	Cercopithecus aethiops aethiops, Erxleben 1777. Cercopithecus aethiops pygerythrus, F.Cuvier 1821.

Cercopithecus aethiops sabaeus L. 1766.
Cercopithecus aethiops tantalus, Ogilby 1841.
Cercopithecus aethiops cynosurus, Scopoli 1786.

The population of Lolui was considered to belong to the subspecies Cercopithecus aethiops pygerythrus F. Cuvier 1821, and that of Chobi to C.a.tantalus Ogilby 1841.

The description of C.a.pygerythrus translated from Dandelot's description is as follows,

> "Face black. Brow band pure white and not separated from the sidewhiskers by fur of a different colour. Sidewhiskers comparatively short and merging gradually with the fur of the top of head. The four extremities and the tip of the tail are black, or a darker colour than the rest of the body fur. A tuft of bright red is always present under the base of the tail. Scrotum a bright turquoise blue." (c.f. Plate 1).

The description of C.a.pygerythrus given by Dandelot fits the Lolui population almost exactly. The only significant variation being the red fur under the base of the tail, which has been already shown to be undiagnostic when considered in isolation. The black colour of the face was observed to vary between a deep purplish-brown and a dark intense black; these differences were not correlated with age or sex. White crescents under the lower eyelids (Plate 2) were observed in many members of the Lolui population, and were most common in lighter faced individuals. The eyes are brown with no white area normally visible. The

Plate 1. Adult male Cercopithecus aethiops pygerythrus, Lolui Island. Note black face, width and shape of brow band, length of sidewhiskers and the way they merge with the fur of the top of the head. Posture is a medium-intensity threat, the vocalisation a low-intensity honk.

teeth are white or yellowish white. In adult males the maxillary canines reach about one inch in length with the mandibular canines somewhat shorter.

The sidewhiskers, which are continuous with the brow band, and which extend as far back as the ears, are white or yellowish white, merging with the fur at the sides and top of the head. The hands and feet are covered with black fur, which extends for varying distances up the limbs. The dorsal surface of the tail for the distal six or eight inches is also black. The top of the head and the back is light grey-brown in colour, but this is somewhat variable between greenish brown to pure grey. The outer surfaces of the limbs and the tail tends to be predominantly a pure light grey, especially in adult males which are also rather heavily furred. In adult females there is less distinction between the fur of the back and that of the outside surfaces of the limbs.

The ventral surface, from under the chin and including the inside surfaces of the limbs, as far as the base of the tail is predominantly white, varying from a yellowish white to pure white. The inside surface of the hinds limbs of adult females between the knee and the genital area may be a bright orange colour, although this was never seen in adult males. One subadult female and one adult female of Group 1 had this characteristic orange fur. The midline between the anus and the scrotum in adult males often included some yellow fur which occasionally culminated in a tuft of yellow hairs surrounding the scrotum; this may be homologous to the orange fur seen in a similar position in adult females.

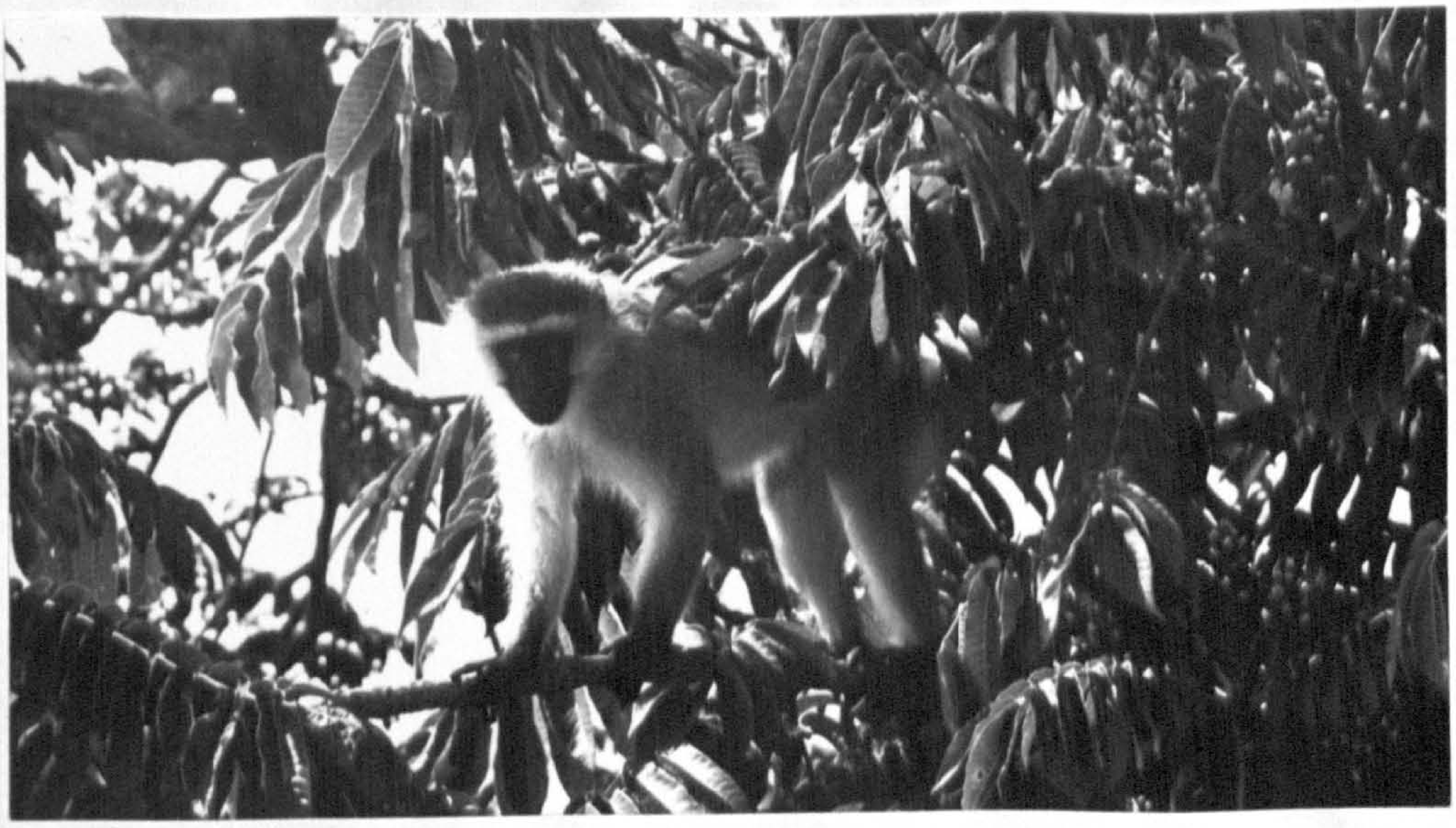


Plate 2. Adult male <u>C.a.pygerythrus</u> standing in normal branch-walking posture in <u>Canarium schweinfurthii</u>. Note white fleck under each lower eyelid, black hands and feet and the white fur on the inside surfaces of the limbs.

Under the tail and above the anus of males a strip of red-brown fur was sometimes seen, but was observed in only 15% of the population. The skin around the anal and perineal areas of both sexes is a bright reddish pink. The scrotum colour of the adult males is bluish turquoise and the penis a bright carmine red. Ischial callosities are present in both sexes.

The population studied at Chobi was classified as C.a.tantalus Ogilby 1841. Dandelot's description of this subspecies is as follows.

> "The brow band is pure white, narrowing towards the middle of the face and is separated from the sidewhiskers by a line of dark hairs from the corner of the eye. The sidewhiskers are long and stiff, yellowish, and more or less flecked at their extremities. The colour contrasts sharply with the pure white of the brow band. There is a tuft of white fur at each side of the base of the tail. There is no black tip to the end of the tail. A tuft of orange fur surrounds the scrotum, which is a clear sky blue".

This description fits the Chobi population very closely in the majority of characteristics. Several features may be only diagnostic when considered in association with others. The orange fur around the scrotum, which in this population varied between a dark orange to a yellow indistinguishable from that of the Lolui population is a case in point. The yellow medial line also described for some members of the Lolui population was considered by Dandelot to be diagnostic of C.a.sabaeus. Numerical taxonomy, which would take into account clusters of diagnostic features would seem to provide an appropriate solution to the problems of classification of this group.

Distribution and physical characteristics.

The species group Cercopithecus aethiops is to be found in savanna and open woodland throughout Africa; from Senegal to Ethiopia and Somalia, and from the Sudan to the tip of South Africa (Fig. 1). The distribution indicated in Figure 1 is based on information in the literature (Dandelot, 1959; Tappen, 1960), data obtained by personal enquiry (C.K. Brain, pers. comm.; T.S. Jones, pers. comm.), and is in part estimated from appropriate vegetational areas indicated in Keay (1959). The distribution suggested here cannot therefore be considered as definitive; it is unlikely to be seriously inaccurate.

In terms of sheer numbers the common vervet monkey is probably the most numerous non-human African primate, although perhaps second to the baboons in terms of sheer biomass. It occurs in a variety of habitats, the most typical being riverine strip vegetation. The species group is anatomically adapted for the conditions of tree savanna or of fôret claire, although displaying no lack of competence in closed forest conditions.

The northern limit of distribution is the arid zone on the southern boundary of the Sahara desert. The species has been reported from the Air Massif (18°,8°E) by Bigourdan and Prunier (1937), but this is doubted by Dekeyser (1950) who considers the specimen to have been probably a young Erythrocebus patas. The high altitude of Ethiopia which moderates the effect of the climate, and the presence of the Nile extend the limit of distribution further north in this area of East Africa. There are few reliable records as to the precise northern limit of distribution in this region. Emin Pasha (1888) travelling south down the Nile recorded them "for the first time" in the woods around Kawa, at about 14°N. Monod (1963) however, records them "north of Khartoum" which is 16°N. Vegetational information suggests that they may extend even further north in the high mountainous regions of Ethiopia, and on the Senegal coast the limit approaches 20°N.

The species group does not occur in the lowland rain forests of the Congo or the West Coast, and is absent from the desert areas of South West Africa except where there is sufficient water to support vegetation. The Orange River, for example, for the last 200 miles of its course flows through country of great aridity and desolation, yet by remaining in the narrow strip of riverine vegetation, the vervets extend their range to the sea.

Biomes inhabited include high-altitude montane forest (Starck and Frick, 1958) through all types of savanna and woodland, to coastal mangrove swamp in West Africa (T.S. Jones, pers.comm.) and papyrus swamp in East Africa, (Pitman, 1954).

Anatomically the species group is distinct from both the more arboreal members of the genus such as C.mitis, and from the closely related patas monkey, Erythrocebus patas which is adapted for moving long distances fairly rapidly in conditions of more or less open grassland. Data given by Jolly (1964) emphasise this point and indicate the nature of the anatomical adaptations that have been evolved to permit the type of distribution and social organisation observed in the species. Jolly compares the more arboreal guenons, a vernacular term indicating the entire Cercopithecus genus, such as C.mitis, with the vervet and patas monkeys in the following measures.

1. Relative upper arm length.
   This dimension showed an increase with increasing terrestriality. There was, however, no significant difference between C.aethiops and E.patas, and that between C.aethiops and the arboreal guenons was demonstrable only at the 5% level of significance.
2. Relative lower arm length.
   This dimension showed an increase in the more terrestrial forms, but in this case C.aethiops was not significantly different from the arboreal guenons, whilst differing strongly from E.patas.
3. Relative total arm length.
   As is to be expected from dimensions 1 and 2, this index also shows a marked increase in the more terrestrial forms. The difference between C.aethiops and the more arboreal guenons is however only just demonstrable at the 5% level.
4. Length of foot relative to lower leg length.
   The more arboreal guenons had significantly higher values for this index. The difference between C.aethiops and the more

arboreal guenons could not, however, be shown to be significant.

5. Relative total leg length.
   This index was significantly greater in Erythrocebus than in the arboreal Cercopithecus species. The C.aethiops series of specimens could not be shown to be significantly different from either the patas or the more arboreal guenons.
6. Lower to upper leg ratio.
   This measure indicated a significantly smaller ratio in C.aethiops than in either the terrestrial patas monkey or the more arboreal guenons.

The conclusion to be drawn from these comparisons is that C.aethiops although in most respects intermediate between the terrestrial patas monkey and the more arboreal members of the genus, is not primitively unspecialised. There is, in fact, evidence to the contrary: the lower to upper leg ratio, smaller than in both more arboreal and more terrestrial species, is evidence of anatomical specialisation permitting easy climbing of trees; an adaptation of clear importance to a species living in an environment with a considerable amount of variability in the horizontal component.

It is not possible from fossil and antomical material at present available to state the definite or probable time scale of the evolution of the species, nor the evolutionary relationships of present species. Freedman (1957) for example has collected a wealth of fossil material from the Transvaal caves, yet specimens likely to be ancestral to the Cercopithecus genus are strangely lacking, suggesting either a rather rapid evolution, or variations in distribution and paleoecology for which there is as yet little evidence.

Evidence from chromosome studies of the *Cercopithecus* genus has added only little to what is known from anatomical or morphological studies. Bender and Chu (1963) however noted that the genus is divisible into three distinct groups on the basis of chromosome complements. The first of these three groups includes *C.aethiops*, *C.diana* and *C.neglectus* and has a diploid number of 60 chromosomes. The second group, comprising *C.mona* and *C.nictitans* has 66 chromosomes. The third group comprises *C.l'Hoesti* and *C.mitis*, both having 72 chromosomes, the highes diploid number yet recorded in any primate.

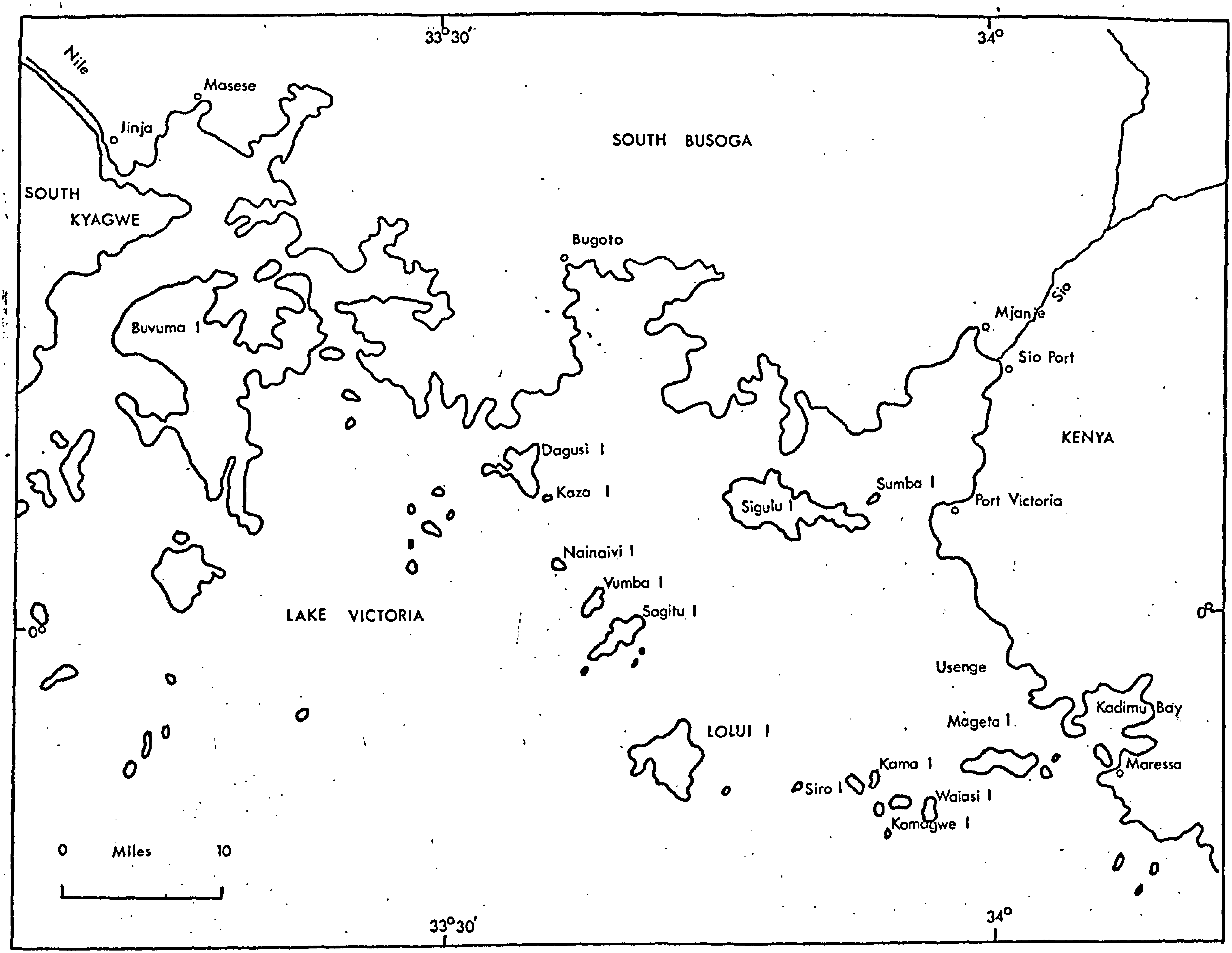
These authors further state that smaller or larger numbers of chromosomes can arise during the course of evolution with little gain or loss of chromosomal material. They suggest, however, that it is more common for the number of chromosomes to decrease during the course of evolution rather than the opposite; a tendency which they state to have been noted in other mammalian groups and in *Drosophila*. From this evidence it seems probable that *C. mitis* does in fact represent a more primitive type than does *C.aethiops*, supporting the view that the latter is a more recent and more specialised evolutionary development.

Location and description of study sites.

The main study site was Lolui Island, Lake Victoria, Uganda (Fig. 2). This island lies in the north east corner of the lake,

Fig. 2.

The islands of north-east Lake Victoria



at the apex of two distinct chains of islands, one extending south-south-east from the Busoga coast through Dagusi, Kaza, Nainavi, Vumba, Sagitu and Masiwa, the other extending west from Kadimu Bay through Mageta, Waisasi, Komogwe, Kama and Siro. Lolui stands apart from both these island chains, being separated from each by between five and eight miles respectively of open water and relatively deep channels (Admiralty Chart: North Nyanza, 1912). To the south and south west lie between 150 and 180 miles respectively of open water, unbroken until the Tanzania coastline is reached. The island is about 25 miles from both Kenya and Uganda mainlands to the east and north-north-west respectively.

Lolui is uninhabited and has remained so since 1908 when the colonial government evacuated the human population in an attempt to stem the effects of the trypanosomiasis epidemic which affected the majority of the islands and the lacustrine coastal areas. It has remained officially a closed area to the present, but in fact is visited occasionally by groups of transient fishermen from both Kenya and Uganda, and also supported a small group of refugees during the Mau Mau emergency in Kenya during the 1950's.

Observations on the island population of C.aethiops were begun on April 23rd 1963 and continued until May 23rd 1964. Six study periods of three to four weeks duration each were spent on the island, and a total of 1472 observation hours was logged. The observations made on Lolui were supplemented by a brief study of another population of the species at Chobi, some 200 miles north of Lolui on the north bank of the Nile, 32° 10'E., in the Murchison Falls National Park. About 120 observation hours were spent on this population. Group counts were also made in the Nairobi National Park and the Masai Amboseli Reserve, Kenya. Other information on this latter point was also provided by C.K. Brain of the Transvaal Museum, Pretoria for Rhodesia and South Africa, and by T.S. Jones for West Africa. A small captive group was also set up and observed at the Department of Zoology, Makerere University College, Uganda and later transferred to Bristol for further observation and experiment.

Geological and geomorphological evidence indicate that in the middle-late Pleistocene the landscape of the Lake Victoria plateau became partly submerged as a result of the back-tilting of the drainage due to warping (Bishop and Posnansky, 1960). Warping apparently continued after the formation of the lake (Bishop, 1958) and the last motions may have coincided with the development of the Nile outlet at the new lowest point of the watershed. This development and the consequent redirection of the drainage of the area must have been the main cause of reducing the level of the lake to close to its present height.

Lolui Island itself is covered with a discontinuous layer of superficial deposits. Apart from this, it is entirely composed of a massive, pale, coarse grained granite which is rich in quartz. This is well-exposed over most of the island, but particularly round the margins where it frequently forms spectacular tors

(Plate 3). The highest point of the island is such a tor which rises to almost 4,000' above sea level and which is situated on the southern peninsula of the island.

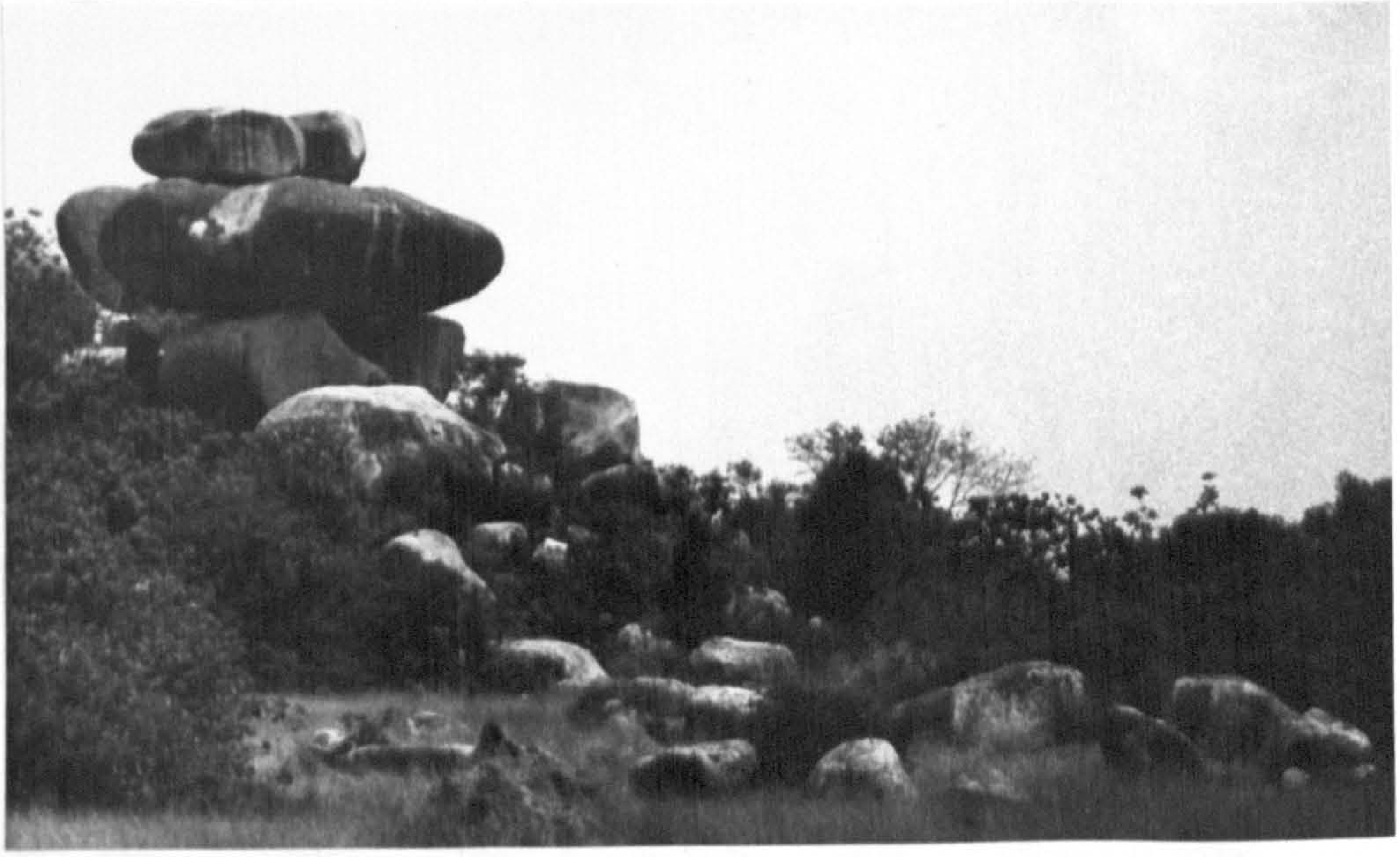


Plate 3. Tor on the north-west peninsula of Lolui Island. The location is on the boundary between the territories of Groups 2 and 8. The rocks are granitic and the site includes rock gongs and rock paintings.

Archaeological evidence indicates two distinct periods of occupation. The first of these was during the Middle Stone Age, about B.C. 40 - 10,000. At this time contact with the mainland was apparently fairly easy and many of the stone artefacts found on the island are manufactured from non-indigenous materials such as banded shales or phonolitic lavas. The nearest probable origin of these materials is the Kenya mainland to the north-east. It seems reasonable to assume, both from the large numbers of these artefacts and from their primitive nature, that there were land connections to the mainland at this time. The fauna and flora of the island has therefore presumably not been isolated for longer than this geologically short period, and with a lake as shallow as Lake Victoria, relatively minor fluctuations in level due to rainfall variations or tectonic movements with subsequent temporary land bridges are always a possibility.

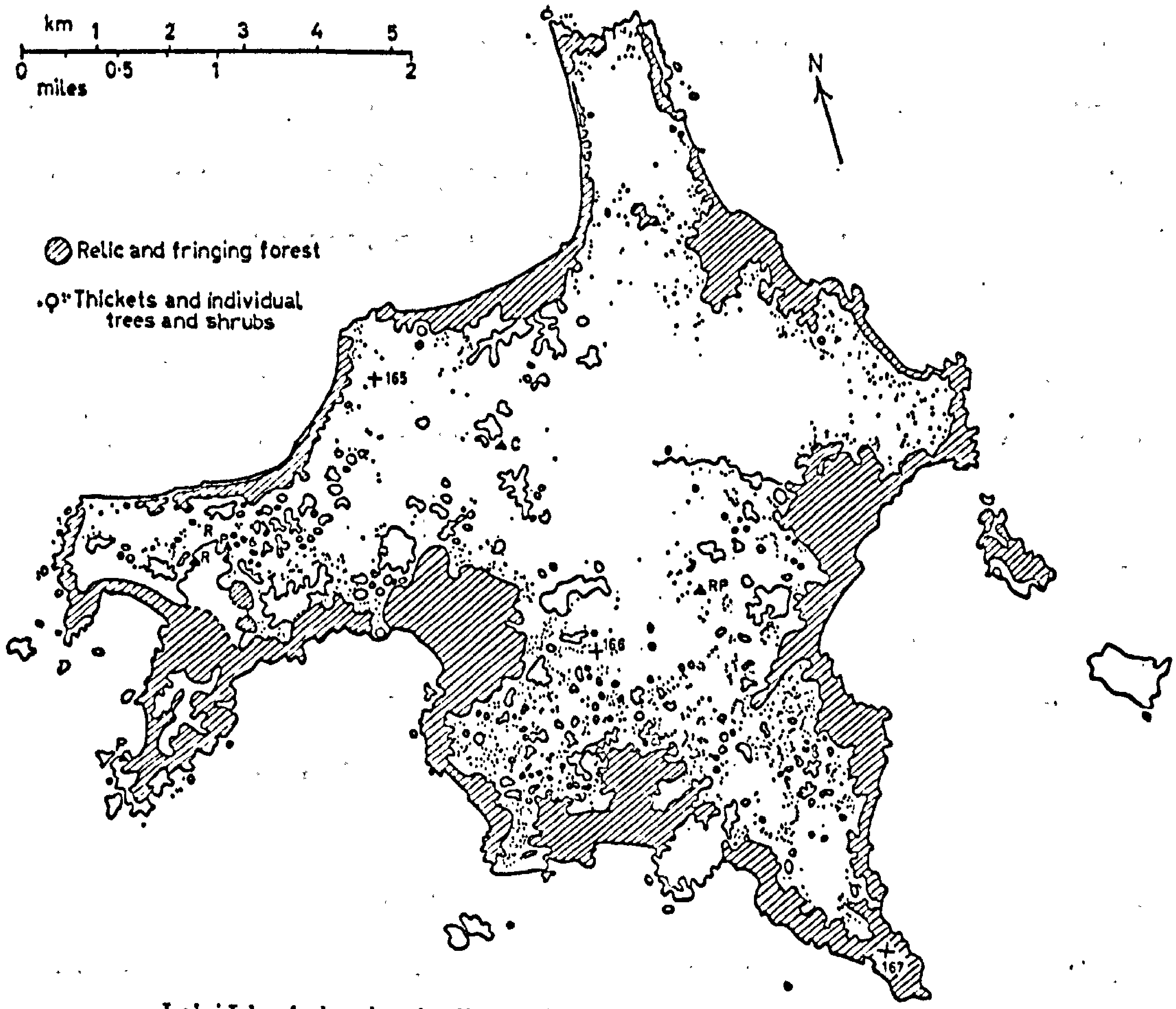
The second period of occupation was during the Iron Age (Posnansky, pers. comm.). A little slag was found during the course of the study indicating that some smelting of metal had been carried out on the island. The pot types discovered indicated a dimple-based type of culture which was initially fairly sophisticated but which later underwent devolution. The dating of these pot types depends on very few firm dates, but indications are that this second period of occupation should be fixed at some time during the last quarter of the first millenium A.D. The devolution of the dimple-based wares indicates a period of cultural isolation between the end of the first millenium until the second half of the second millenium A.D., when Entebbe wares make their appearance. (Posnansky, pers. comm.).

The discovery of Busoga wares around the coastal margins of the island indicates an increased contact with the Uganda mainland during the nineteenth century; a finding which is compatible with the known facts of the history of feuds between the Kabakas of Buganda and the island of Buvuma towards the end of the nineteenth century. This increased contact probably continued until the evacuation of the island in 1908.

The period of cultural isolation during the Iron Age meant that the island must have been necessarily self-supporting. Fish would have been readily obtainable as a source of protein; today four main species are caught by native fishermen, _Bagurus_, _Mormyrus_, _Haplochromis_ and _Tilapia_. Archaeological evidence such as grinding holes for millet and extensive field systems indicate a great deal of indigenous cultivation. This fact and other less direct effects of the heavy population pressure must inevitably have had serious effects on the indigenous flora and fauna. Johnston (1904) records "above 100 per square mile" on Lolui in 1901. Many of the forest species must have been eliminated and many of the remaining ones restricted to small areas of relic forest (Fig. 3). Today, although the island is extremely poor in the number of species of both flora and fauna found there, individual species are very common; a pattern which is directly related to the interaction of the flora and the mammalian fauna, particularly the monkey population, during the seral stages of succession.

Fig. 3.

(From G. Jackson & J.S. Gartlan, 1965).



Lolui Island, showing the distribution of thickets in relation to the fringing and relic forest, and archaeological sites of importance. +, Optical centres aerial photos 44/UG 33/6 February 1960, Alt. 24000 ft (7300 m)/6 in. lens. ▲, Archaeological sites: R = rock gongs; P = paintings; C = cairns.

Equipment, techniques, definitions and terms.

The equipment used in this study was of two types; that concerned with ecological assessment and that with the recording and measurement of behaviour.

For the former purpose equipment used included plant presses, collecting jars, formalin and alcohol, a mist net, a drill for obtaining soil samples, tape measures, compasses, small mammal traps, a sweep net, collecting tubes and a small dissecting kit. For the observation and recording of behaviour a pair of Delacroix 10 x 50 binoculars was used, a stopwatch, a Practika 35 mm single lens reflex camera which gave unsatisfactory results due to a faulty film transport system and an inaccurate focal plane shutter. Three lenses were used, an f2.850mm lens, a f2.8 135mm and a fixed focus f8.0 500mm lens. Unfortunately a wide-angle lens was not available. Lens hoods and ultraviolet filters were used. Some colour cine film was taken using a Bolex 16mm reflex cine camera; the results were not good, due to a fault in the turret rotating system which led to light leaks and damaged film. A Weston lV exposure meter gave satisfactory service. A Fi-Cord 201 portable tape recorder was used with a Grampian D.P.4. microphone and parabolic reflector, but serious faults rapidly developed which could not be rectified in East Africa, and no good quality recordings were obtained.

Field notes were initially recorded in waterproof surveyors' notebooks, but this was found to be an unnecessary precaution and subsequently ordinary "shorthand" notebooks were used. All field notes were revised at the end of the day and copied onto cards using a preliminary classification. The main categories were:

A. Numbers and classes of animals.
B. Behaviour towards the observer and other individuals.
C. Behaviour towards other animals.
D. Locomotion and postures.
E. Day resting and ranging.
F. Feeding and food items.
G. Social grooming and self-grooming.
H. Play
I. Sexual behaviour.
J. Grouping behaviour.
K. Vocalisations.
L. Weather and climatic conditions.
M. Maternal behaviour.
N. Other social behaviour.
O. Developmental information.
P. Birth information.
Q. Aggression.
R. Territorial behaviour.
S. Individual idiosyncracies and miscellaneous information.

During the first month (April - May, 1963) a preliminary survey of the island was carried out with the late Professor K.R.L. Hall. The primary aim of this survey was to establish the suitability of the site for a long-term study of the species. No quantitative measures of ecological factors were attempted. The collection of botanical specimens was begun, a general survey of the fauna of the island was carried out, the presence of rock paintings and carvings was noted and the collection of archaeological material begun.

Subsequent to this initial survey, the ecology of the island was analysed in more detail. The botanical and archaeological collections were maintained, attempts were made to trap small mammals and soil samples were taken. The general picture of the island ecology so obtained was supplemented by more detailed studies with the aim of establishing the precise role of the monkey population in the reforestation of the island. Monkey faeces were collected, weighed and analysed, the species composition of vegetation thickets was analysed, and data on food seasonality and the population density of the monkeys was obtained.

In April 1964 the author was accompanied to Lolui by Mr. George Jackson, formerly of the Department of Agricultural Biology, Makerere University College. During this study period detailed analysis of the species composition of the island flora and fauna were carried out and compared with data for other similar sites. The details of the reforestation process were confirmed, and an analysis made of the grassland types.

Although surveys of the entire population of Lolui were attempted to establish details of the seasonality of births, population density and the range of group sizes and age-sex structure of groups, the majority of behavioural observations were carried out on the north-west peninsula of the island (Fig. 3). No attempt was made to mark individual animals or to interfere with them in any way. The aim of the observer was to become a neutral part of the environment. One feeding experiment was carried out during the later stages of the study to examine the results of artificial feeding on a group (Group 2) on which the normal social structure and patterns of interaction had already been established.

Individual recognition of many animals was possible. Adult females were most easily recognisable by features such as the length and colouration of the nipples; they were also rather variable facially and after some acquaintance, identification could be confidently made on the basis of facial and postural differences. Adult males were more difficult to recognise, but often black, freckle-like marks on the scrotum provided some clue at fairly close range. White flecks underneath the eyelids (Plate 2), the variable yellow medial line between anus and scrotum, and the occasional presence of the red-brown bar under the base of the tail also provided means of recognition. Wounds were not generally of use (c.f. Brain,1965) as they were rare and generally not severe. Some males could be identified by aberrant voices. The animals most difficult to identify individually were infant twos and young juveniles, but sometimes recognition was possible.

Behavioural observation was generally begun, at, or soon after sunrise and continued throughout daylight. The pattern of observation varied with the particular problems being studied. When day ranges were being established the entire day would be spent with groups following and recording progress on sketch maps.

Alternatively, several groups would be sampled at intervals of about an hour so that successive positions were obtained. Time samples of the activities of group members were occasionally taken throughout the study, the usual period between observations being fifteen minutes.

All animals in the north west peninsula became tame enough not to exhibit escape behaviour at the approach of the observer. However, alarm chirrups and chitters, and occasionally adult male honks were still given by groups on which the main behavioural observations were not carried out until the end of the study. Sudden movements did alarm even habituated groups, as did drastic changes of clothing on the part of the observer, such as the sudden donning of a long black plastic raincoat in place of the usual shorts and khaki shirt.

The following age-sex categories are used in this report.

1. Adult male (AM)
2. Adult female (AF)
3. Subadult female (SF)
4. Juveniles (JM or JF)
5. Infant two (I2)
6. Infant one (I1)

The behavioural and morphological criteria used to define the categories are as follows.

1. Adult males.

This category has the adult colouration of the pelage. The scrotum is turquoise blue rather than the more purple colour seen in juvenile males, and the testicles are fully descended. The scrotum is pendulous. Maxillary canines are fully developed and prominent; Weinbrenn (1930) gives a mean length of 2.5cm for this tooth in adult males. The voice is deep. Behaviourally they are more phlegmatic than juvenile males, only coming to investigate a disturbing stimulus causing juvenile males and adult females to chirrup and chitter after these vocalisations have persisted for some minutes. They are more likely to be found away from the main body of the group and away from other individuals. The mean weight of two adult males of the captive group was 12 lb. 1 oz. The mean body length of six individuals of the subspecies C.a.pygerythrus given by Pocock (1907) is, head and body length 456mm, tail length 584mm. Age is 5 years plus.

2. Adult females

There are no externally visible signs of the onset of sexual maturity in females of this species comparable to the changes observed in adult males. There is no sexual skin and external signs of menstruation are rarely observed. In this report therefore the term adult female refers to animals which, from the condition of the nipples can be concluded to have borne at least one infant. Lengthening of the nipples occurs after only one or two days of suckling by the infant.

The behavioural criteria are not clearly differentiated from those of subadult females. Maternal behaviour does not appear to be essentially different from "aunt" behaviour, except that in the latter suckling by the infant was never observed. Adult females also show "aunt" behaviour (Rowell, 1963). This age-sex group is not generally found away from the main body of the group or from other animals.

The mean body weight of three adult females of the captive group was 7lb 9 oz. The body length of the only adult female noted by Pocock (1907) was, head and body 403mm. The age of this category is 3½ years plus.

3. <u>Subadult females.</u>

Subadult females are physically mature, but are nulliparous. For the purpose of field identification this means that they lack the elongated, pendulous nipples of adult females.

Behaviourally, they are very likely to be involved in "aunt" behaviour; they also occasionally play with infants in the normal play-bite pattern, but this is rare. They copulate in the normal manner with adult males and participate in social grooming in approximately the same patterns as do adult females. In size they are similar to adult females. Pocock given no measurement, and there were no subadult females in the captive group. The age of this category is between 2½ and 3½ years.

This category was not used during the early part of the survey when population surveys and group age-sex structure assessments were being made.

4. Juvenile males.

The transition between juvenile and adult as far as males were concerned was distinct and fairly rapid. The category of subadult for this sex was not therefore considered necessary. The testes are not properly descended in this age-sex category, and the scrotum is purplish rather than the adult turquoise colour. The canines are not fully developed, although they are distinct. The voice is usually high pitched. They are not detached from the group and independent of other animals in the same way as are adult males, although tendencies in this direction become apparent with increasing age. They are capable of penile erection and copulation but rarely achieve ejaculation, and the criterion of complete copulation, the ejaculatory pause, was never reached by a juvenile male.

They appear to have a distinct role in the vigilance behaviour of the group, in that they given alarm chirrups and other chitters more frequently and more persistently than other age-sex categories. The number of juvenile males in a group determines to a large extent the reaction of the group to the approach of the human observer.

The age of this category is from 18 months to 5 years. The mean weight of two juvenile males in the captive group was 6 lb. 5 oz.

5. Juvenile females.

This age category of females does not show the interest in infants of the same pattern and intensity shown by subadults and adults. Like juvenile males, they are less tolerant of the approach of intruders, giving frequent alarm chirrups and chitters, although the patterns observed in juvenile males were not as pronounced in this category. The age of this category is from 18 months to 2½ years. No information on weight or body length is available.

6. Infant twos.

This age category is predominantly peer-orientated. They are weaned and largely independent of the mothers, although returning to them in times of danger. They show the adult patterns of colouration, but the pelage is generally somewhat lighter. They begin to make competent grooming movements of other animals. This category shows much play and exploratory behaviour. The age of the category is between 5 and 18 months.

7. Infant ones.

Infant ones are primarily mother-orientated. They are born with pink faces and ears and a dark brown pelage and are completely dependent on the mother. They are unweaned, but by five months are taking a large amount of vegetable food in their diet. They return to the mother readily, not only in dangerous situations, but at regular intervals during play behaviour. The age at which this category is appropriate is from birth to 5 months.

In this report the category of "group" is used to denote a clearly discrete unit subject to boundaries of the frequency and type of communication and interaction. A group is restricted to a particular geographical area, although adult males are observed to change between groups.

The distinction between "territory" and "home range" raised by Burt (1943) was found useful in this study. Territory is here used to denote the area in which a particular group is normally found, which is behaviourally distinct, in that animals leaving it exhibit a change in behaviour from "owners" to "trespassers". It is a defended area in that it is marked and that intruders are driven out.

These criteria, it was found, did not apply to the Chobi population which cannot be said to be territorial. A differential use of "core areas" within the territory was not observed in the Lolui population, the main reason almost certainly being the small size of the areas involved. There was a differential use of the territory in alarm and threat behaviour. Alarms and threats at the human observer, and often in inter-group disputes would only take place in trees or thickets and not usually in open grassland.

Other terms and definitions used in the text are defined when first used. In view of the conclusions reached at the beginning of this section concerning the concept of "social dominance", the concept will not be used in this report. Further reasons for this, and supporting experimental and behavioural evidence will be given in the section on social behaviour.

THE ECOLOGY OF LOLUI ISLAND.

Recent history of Lolui Island.

A brief summary and discussion of the history of Lolui Island was given in the introductory section. More detailed evidence of recent changes important in determining the present state of the Lolui ecosystem will now be discussed.

Field systems of recent origin consisting of earth banks, presumably as a measure to check soil erosion, and lines of stones as boundary markers are a prominent feature in the northern part of the island (Plate 4). The banks frequently follow the contours and are continuous for upwards of several hundred yards. They are not higher than three feet and are generally from one to two feet high. The lines of stones, which are very common, are striking in their regularity. These are often broken grinding stones set up on edge, between five and fifty feet apart, with a mean distance between them of 20-30 feet. These factors, together with the very numerous grinding hollows which occur on most small rock piles, tend to indicate an intense indigenous cultivation of grain, probably millet, between the end of the first millenium A.D. and the time of evacuation. The hollows (Plate 5) are found all over the island except in the very rocky areas of the southern promontory which was presumably unsuitable for human occupation; they vary between half an inch and two and a half inches in depth and are up to two feet long and fifteen inches wide. They vary in shape between square, through oval to circular. In places there are more than thirty such hollows on a single rock. They are also found in thickets overgrown by vegetation indicating that the thickets postdate the grinding hollows.

At the time of evacuation therefore, the land that had been cleared for agricultural purposes was susceptible to the normal processes of ecological succession, and the present state of the island ecosystem has clear roots in the historical accidents affecting the island. The present vegetation communities of the island may therefore be considered in four main categories; original and relic, derived, regenerative and invasive.

Plate 4. Line of boundary stones exposed in grassland that has been cleared by burning. The line is in the middle foreground running diagonally from left to right. Note the variation in the size of the stones used.

Climate

Data on rainfall recorded on Lolui during the study was found to be inaccurate and was discarded. Field information on weather and climatic conditions was however recorded routinely throughout the study period. Comparison of these records with daily climatic information for Entebbe, ($0^{\circ}03'N$, $32^{\circ}27'E$) on the northern shore of the lake showed a broad similarity between the two locations. Information collated by the meterological service of the East African Common Services Organisation also showed similar patterns of precipitation and temperature between the two areas. Lolui is surrounded by open water subject to squalls and the climate must be modified by this to a certain extent.

Plate 5 Grinding hollows located on a small rock in the north-west peninsula. Note the depth and shape.

Climatic data for Entebbe, Buvuma Island ($0^{\circ}11'$N, $33^{\circ}18'$E), Lwazimirule, Kome Island ($0^{\circ}05'$S, $32^{\circ}47'$E) and Kisumu ($0^{\circ}06'$S, $34^{\circ}45'$E) are shown in Table 5. From the means, the zone in which Lolui lies is likely to have an annual mean rainfall of 60 - 65 inches, with 100 - 150 rain days per year, an annual mean maximum temperature of 27.5°C and an annual mean minimum temperature of 16°C. There is no month completely without rain, although the period March to May is wetter than other times of the year with frequent thunderstorms, particularly in late afternoon and evening (Plate 6). There is a second peak of rain in November and December. The climate favours the type of forest designated by Langdale-Brown, Osmaston and Wilson (1964) as moist semi-deciduous.

Geology and geomorphology.

Lolui is a low lying feature, roughly triangular in shape with the shore about 3726 feet above sea level. The centre of the island (3800 to 3900 feet) is a gently rolling plateau with only one semi-permanent stream. Exposed in the grasslands and within the forests are numerous rock outcrops (Plate 3). The rocks forming these outcrops are a pale granite which has a well-marked crystalline structure that on weathering gives rise to fragments about 4mm in diameter. There is considerable shallow exfoliation on the exposed rock surfaces and many of the larger groups of rocks show evidence of splitting due to stress. The exposed rocks often constitute striking formations in which rock gongs and paintings are found. (Jackson, Gartlan and Posnansky,

TABLE 5

Rainfall data for four stations in the latitude of Lolui Island.

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1. Station No. 89.3266. Entebbe Airport, 0°03′N 32°27′E. Altitude 3761 ft (1146 m)													
Mean rainfall (15 years) (in.)	3·60	3·44	6·42	11·24	10·02	3·99	2·60	3·40	3·48	3·90	5·91	5·08	63·08
(mm)	91	87	163	285	255	101	66	86	88	99	150	129	1600
Rain days (1962)	12	8	19	22	23	15	8	16	8	20	9	10	170
Rainfall (1962) (in.)	3·26	2·75	8·64	7·98	11·73	1·90	1·66	6·57	2·75	9·50	3·18	2·93	62·85
(mm)	83	70	219	203	298	48	42	167	70	241	81	74	1596
2. Station No. 89.3305. Buvuma Island, 0°11′N 33°45′E. Altitude 3800 ft (1150 m)													
Mean rainfall (28 years) (in.)	3·60	4·30	7·56	9·40	9·96	3·82	2·81	2·67	2·93	3·62	5·67	5·53	61·87
(mm)	91	109	192	239	253	97	71	68	74	92	144	140	1570
Rain days (1962)	9	3	13	16	18	8	2	7	5	9	3	6	99
Rainfall (1962) (in.)	6·44	1·59	5·61	14·02	11·04	6·10	0·87	2·74	2·75	9·17	1·86	3·39	65·58
(mm)	164	40	142	356	280	155	22	70	70	233	47	86	1665
3. Station No. 90.3425. Kisumu Met. Stn., 0°06′S 34°45′E. Altitude 3769 ft (1147 m)													
Mean rainfall (15 years) (in.)	2·14	2·86	6·27	7·60	6·65	3·96	2·67	3·84	3·01	2·49	4·16	4·16	49·81
(mm)	54	73	159	193	169	101	68	98	76	63	106	106	1265
Rain days (1962)	11	3	16	18	20	15	14	12	14	15	10	11	159
Rainfall (1962) (in.)	4·52	0·40	6·94	9·80	14·09	4·26	2·53	2·09	4·95	3·22	4·92	3·43	61·15
(mm)	115	10	176	249	358	108	64	53	126	82	125	87	1553
4. Station No. 90.3209. Lwazimirule, Kome Island, 0°05′S 32°47′E. Altitude 3800 ft (1150 m)													
Mean rainfall (17 years) (in.)	5·11	4·55	8·40	12·00	12·41	6·28	4·90	3·87	4·02	4·75	8·51	8·33	83·13
(mm)	130	116	213	305	315	160	124	98	102	121	216	212	2112
Rain days (1962)	17	8	16	18	21	5	6	8	5	9	9	7	129
Rainfall (1962) (in.)	10·38	4·73	9·16	8·30	18·29	6·47	6·14	6·27	4·65	9·15	7·80	10·61	101·95
(mm)	264	120	233	211	465	164	156	159	118	232	198	269	2589

From Jackson & Gartlan, 1965.

1965).

Plate 6. Typical thunderstorm blowing up from the lake, late afternoon, April 1963.

The soils of the island presumably derive from the weathering of the overlying sedimentary rocks, which is now complete, and from breakdown of the parent granite. They are ferralitic and range from yellow-red sandy clay loams to coarse sandy loams, (J. Harrop, pers. comm.). Towards the coastline and in depressions, wash from higher points has given rise to soils which are much sandier in texture and which are grey-brown in colour with a pale sandy surface.

Vegetation.

Forest

There are six major areas of moist semi-deciduous forest, largely confined to the rocky areas of the island (Fig. 3). The forest contains trees up to 120 feet tall, is dense and shows considerable regeneration of many species. As in all tropical semi-evergreen forest, it is difficult to achieve complete listing without felling, but the common species were identified by means of fallen leaves, flowers, fruit and slash characters. The two commonest high canopy forest trees are *Markhamia platycalyx* and *Canarium schweinfurthii*, the fruit and leaves of the latter being a major component of monkey diet. There is a well developed shrubby understorey and a tangle of lianes and creepers such as *Saba florida*, *Uvaria virens* and *Agelaea ugandensis*. On the forest floor there were several grasses of typical forest habitat such as *Pseudechinolaena polystachya*, *Oplismenus hirtellus* and *Panicum brevifolium* and various forest herbs including *Sansevieria* sp. in pure dense stands, *Haemanthus multiflorus* and *Desmodium adscendens*. Four species of fern are also commonly found, and in the forest these are usually found associated with rocks or termite mounds.

Fringing forest

Along the lake margin between the coast and the grassland there are belts of forest which have at one time carried extremely tall forest vegetation (Plate 7). The rise in lake level following recent seasons of heavy rain has caused flooding in these areas and in many of them individual trees have been killed by waterlogging. Where fringing forest was replaced by grassland the same effect was seen on grasses which were drowned. The composition of the fringing forest was assessed and *Canarium schweinfurthii* *Maesopsis eminii* and *Antiaris toxicaria* found to be prominent. *Garcinia huillensis*, *Popowia buchananii*, *Uvaria virens* and *Canthium vulgare*, all species providing common monkey foods are found in the understorey. At the edges of the fringing forest the shrub *Alchornea cordifolia*, forms an almost impenetrable stand. The ground cover is often sparse or lacking, but on the north coast, areas of *Alchornea* thicket carry a ground cover which includes elements of the forest flora.

Thickets

Scattered over the island are thickets of varying size and density which have a characteristic flora and appearance. They are important habitat areas for the monkey population, and indeed these animals play a large part both in their origin and floral composition. The most commonly found types are as follows:

a. Thicket dominated by one or a few tall *Canarium schweinfurthii* trees. The dominant tree is often of large proportions being up to 40m. tall and 1.7m in diameter at chest height. Surrounding the main tree are *Garcinia huillensis*, *Vitex fischeri*,

Plate 7. Fringing forest on the north-west peninsula. Note the rocky substrate; tree at right is <u>Canarium schweinfurthii</u> showing typical profile.

Pachystela brevipes and *Maesopsis eminii* which form a dense, low-branched cover at the thicket edges. Within the thicket the lower branches die and are destroyed by termites. If there is not too dense a tangle of lianes at ground level it is fairly easy to move about inside the thickets. At the margin of these thickets *Harungana madagascariensis* and *Popowia buchananii* are established, with the herbs *Erlangea tomentosa*, *Urena lobata* and *Triumfetta rhomboidea* at the edges of the woody vevetation. The grass *Eragrostis blepharoglumis* forms a belt between the thicket proper and the surrounding grassland, indicating a different microclimate in this particular area, a point of importance in the ecology of the reforestation process, the significance of which will be described later. (Fig. 4).

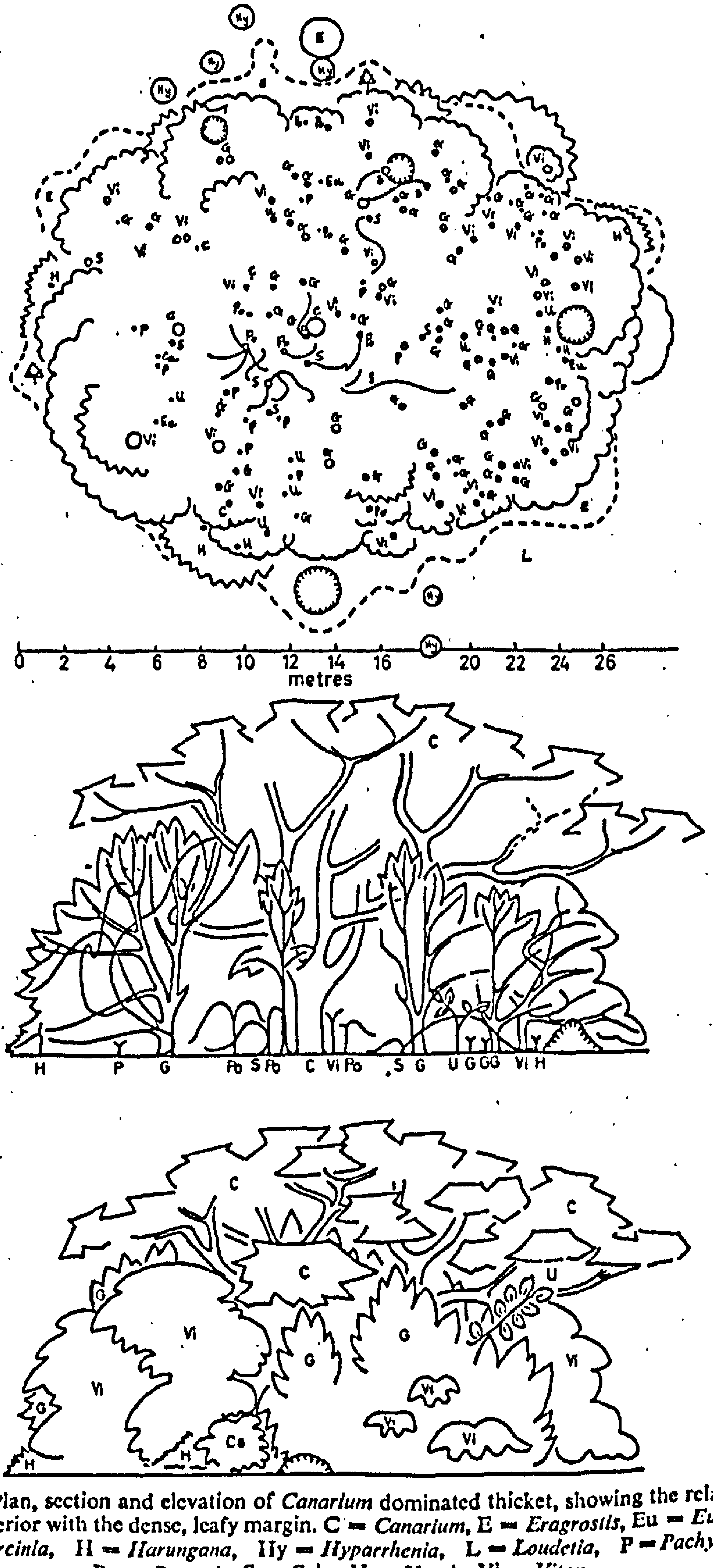
b. Thickets without dominant *Canarium*.

In these thickets (Fig. 5) *Vitex fischeri* and *Garcinia huillensis* are particularly common in the north-west promontory of the island, where the majority of the behavioural study was carried out. *Bridelia micrantha* and *Alchornea cordifolia* assume greater prominence in damper areas. *Harungana madagascariensis* is invariably found at the edge of thickets.

Canarium schweinfurthii is often present as seedlings or saplings and appears to do well in this habitat. Also found are seedlings of *Antiaris toxicaria* and *Ficus* spp. In both thicket types described the creeper *Saba florida* is common and spreads from the margins of thickets into the surrounding grassland by means of long prostrate woody stems, "pseudostolons". Thickets are

Fig. 4

(From G. Jackson & J.S. Gartlan, 1965)



Plan, section and elevation of *Canarium* dominated thicket, showing the relatively open interior with the dense, leafy margin. C = *Canarium*, E = *Eragrostis*, Eu = *Eugenia*, G = *Garcinia*, H = *Harungana*, Hy = *Hyparrhenia*, L = *Loudetia*, P = *Pachystela*, Po = *Popowia*, S = *Saba*, U = *Uvaria*, Vi = *Vitex*.

Fig. 5 Thicket type b.

This thicket is typical of the type not dominated by a single large Canarium schweinfurthii tree. It is located in the north-west promontory, in Group 1's territory.

often joined together by this means. (Plate 8). Uvaria virens is also frequently found as a climber.

Plate 8. "Pseudostolons" of Saba florida extending into grassland and joining two adjacent vegetation clumps.

c. Single trees with low undergrowth.

Vitex fisheri, a principal source of food of the monkey population is the most commonly occurring single tree, and is often found established near or on termite mounds or rocks (Plate 9). It has a characteristically rounded profile with branches often reaching the ground. Below the tree various seedlings, including all the common thicket species are commonly found.

Popowia buchananii, Garcinia huillensis, Cararium schweinfurthii and Alchornea cordifolia, all monkey food species, are also occasionally found established as isolated trees.

d. Saba florida

This Apocynaceous climber becomes established from seed in open grassland, but more usually in association with termite mounds or at the base of low rocks. When fully established it forms dense thickets up to 3m. tall and tends to spread in all directions by means of "pseudostolons". This species, along with Harungana madagascariensis and Vitex fischeri forms a major part of the diet of the C.aethiops population. (Plate 10).

Grasslands.

1. Loudetia kagerensis

Loudetia kagerensis forms a low-cover grassland particularly near the shores of the lake where the sand wash has given rise to soils which are particularly sandy. The grass is not strictly confined to this habitat and is found in association with all other grassland types except those on alluvial sites below heavier soils. L.kagerensis

Plate 9. Single _Vitex fischeri_ established on termite mound in _Loudetia kagerensis_ grassland. Note characteristic profile. The darker, greener grass immediately underneath the tree is _Eragrostis blepharoglumis_, a grass of damper, better-drained areas. The shrub on the right of the picture is _Alchornea cordifolia_.

is found in very depauperate form in cracks and crevices in rocks and appears to respond morphologically to soil depth available for growth. It is eaten by monkeys.

2. Andropogon dummeri.

Andropogon dummeri forms a low-cover grassland which is often much grazed by hippopotamus; it is also eaten by monkeys. It is found on the yellow-red ferralitic soils, particularly where the surface sand has been washed into gullies. It is often associated with Loudetia kagerensis and Eragrostis racemosa.

3. Hyparrhenia dissoluta.

Hyparrhenia dissoluta is a tall grass forming low-cover grasslands of limited extent. It is generally confined to the less well-defined drainage lines and the least eroded soils of the central plateau. It is a palatable grass and grazed by hippopotamus, although no monkeys were observed feeding directly from it. H.dissoluta is associated with Andropogon and Loudetia, particularly where it is grazed. The seed heads of this grass are a frequent site of spider webs, which during the occasional swarms of Chironomid lake flies often trap several hundred of these small insects. The seed heads are bent down by grass-ranging monkeys, the webs removed with the hands and eaten.

4. Eragrostis blepharoglumis.

Eragrostis blepharoglumis is a densely tufted grass which gives rise to almost pure stands in the drainage lines and hollows of the island. Elsewhere in Uganda this grass is characteristic of wet areas and of swamps and swamp margins. The densely tufted nature of the grass and the low ground cover has given rise

Plate 10. *Saba florida* established on termite mound in grassland. In the middle distance another sapling can be seen growing in close association with a rock.

to a very uneven ground surface since the tufts themselves are resistent to erosion, and channel the runoff water between them. *E.blepharoglumis* burns fiercely and there is clear evidence that the grass need not be fully dry before a burn takes place. Isolated woody species which are established in this grassland suffer fire damage to an apparently greater extent than those in the *Loudetia* areas, presumably because of the relatively fiercer burn.

5. *Microchloa kunthii.*

This grass forms limited communities on shallow, gravelly soil overlying rock, but on the north coast there is one area where it forms a dense sward as a bottom grass in closely grazed *Loudetia kagerensis.*

6. *Sporobolus festivus.*

Sporobolus festivus is of minor importance on rocks and rocky outcrops.

Fauna.

The fauna of Lolui having been subjected to the same ecological pressures as the flora, shows a pattern of species composition essentially similar to that already described for the flora of the island: relatively large numbers of a small number of species. With the long period of intense cultivation and high population pressure indicated by the archaeological evidence, the climax forest cover was evidently removed. Many forest mammal species would have been eliminated by the destruction of their habitat. Others would have been eliminated probably by direct means such as hunting; this would presumably apply to large predators such as leopard and also possibly to smaller mammals such as monkeys and hyraxes which would provide a source of protein invaluable in an island as isolated as Lolui. These pressures may be assumed to have reduced both the numbers and the species composition of the indigenous mammal fauna and to have restricted those capable of existing under deprived conditions to small areas of relic forest or rocky areas which were unsuitable either for cultivation or for habitation.

With the evacuation of the island in 1908 and the reversion of the cultivated areas to grassland, there were no species such as antelope capable of the efficient exploitation of the new ecological niches. The species colonising the island were in the main those that had managed to survive in the relic forest and rocks; although the introduction of new species capable of movement across the lake barrier is always a possibility; hippopotamus and sitatunga being a case in point. To a large extent, however, the abnormal species composition with a consequent lack of predation and of competition has allowed a great increase in numbers of <u>Cercopithecus aethiops</u> which was the species capable of utilising the seral stages of succession most efficiently. This increase has affected both the rate of the reforestation process which is taking place, and also the pattern and species composition of the new forest areas.

<u>C.aethiops pygerythrus</u> is ubiquitous and by far the commonest large mammal species on the island. It is found wherever there is sufficient tree cover providing shade, sleeping sites and food.

The approximate biomass of the population on the north-west peninsula and the relationships with other species are shown in Fig. 6.

The sitatunga, Limnotragus spekei is not common on Lolui, a fact which is probably accounted for by the lack of papyrus swamp, the normal habitat of the species. It is relatively common on Sagitu, to the north-west of Lolui where papyrus swamp occurs in several places around the coast. On Lolui it is apparently restricted to the fringing forest and Alchornea cordifolia thickets, from which it emerges at night to make feeding expeditions into the grassland. It seems likely that the main food taken on these occasions is grass, but the leaves and fruits of Alchornea cordifolia are recorded by Eggeling (1940) as a common food of this antelope. In this respect there is some slight competition with the monkeys for the Alchornea fruit. The species was never seen, being apparently nocturnal, but the characteristic footprints were observed on several occasions.

The hippopotamus, Hippopotamus amphibius L. occurs throughout the island. It is not as common as in other areas of Uganda, but this does not appear to be because of any poaching activity, deep water offshore and a lack of shelter are more likely to be limiting factors. The species is exclusively herbivorous, spending the day in the relatively shallow offshore waters and emerging at night to make extensive feeding expeditions into the grassland, returning generally by daybreak, although occasional individuals are met with as late as mid-afternoon. Individual animals appear

Fig.6

Species contribution to large mammal biomass, habitats exploited and competitive relationships.

(north-west peninsula only)

to stay in the same area of water during the day, and to emerge by a particular and well-defined path at night. The extensive ranges of the animals made it difficult to estimate how many individuals the north-west peninsula would support. A small group of five individuals regularly spent the day in the water to the north of the north-west peninsula, but no more than two were observed feeding in the north-west peninsula grasslands at night, although the observation conditions were poor and possibly more than this do use the grasslands at some time during the night. The animals that habitually use the grasslands of the north-west peninsula apparently only fed there during the early hours of the night; by midnight it was only very occasionally that they were encountered in this area. As an approximate estimate, it was thought that the area could support about 1.5 hippopotamus. The weight of the species is given by Bere (1959) as over 3,000 lb. Even for this comparatively few animals, the biomass is more than that of the monkey population. The grasslands of the central plateau were rarely grazed by hippopotamus, which apparently preferred to graze as near as possible to the water.

Hyparrhenia dissoluta is a grass that is commonly grazed by the hippopotamus, and in this they are probably not in competition with any other mammal. They also eat other grasses such as Loudetia kagerensis and Andropogon dummeri which does bring them into competition with the monkeys, but not to an extent which is limiting to either species. The amount of hippopotamus grazing on Lolui, although heavy cannot be considered as overgrazing except in certain very restricted areas, and has not led to degeneration of the grasslands and to serious soil erosion on the scale observed in the Murchison Falls grasslands.

The genet, *Genetta tigrina* Schreber, a small nocturnal predator, spends the day in tree cover, emerging at night to feed. It is probable that this species preys on insects and arachnids, and also on small mammals such as mice and shrews. Attempts to trap specimens of the latter were not very successful; five shrews and four mice were caught, each family being apparently represented by a single species, although identification has not yet been completed. The genet is probably in direct competition with the majority of the reptilian predators of Lolui, especially the monitor lizard, *Varanus niloticus*, the puff adder, *Bitis arietans*, the black-lipped cobra, *Naja melanoleuca*, and to a lesser extent the small green snake *Chlorpohis* (?) *heterolepidotus*, all of which feed on essentially the same diet as the genet. Whether the genet population is a limiting factor in the reptile distribution, or vice versa is not known, but it is extremely unlikely in view of the abundance of food species.

The rock hyrax, *Procavia capensis* Pallas occurs on rocks and tors especially in the north-west peninsula; it is not a common species. The diet according to Bere (1962) consists of leaves, bark and small fruits, and in this respect they are in competition with the monkey population. This does not appear to have been the factor limiting the expansion of the population since the time of evacuation. A more likely explanation is the change in habitat which has occurred and which is continuing to take place. The hyrax is only observed in rock tors that are not overgrown by vegetation, which are fairly high, and which incorporate caves; a typical site being that shown in Plate 3. The species was never observed in apparently similar habitats located within the forest. The reforestation since the time of evacuation has probably reduced the number of suitable sites, particularly as rocks and termite mounds frequently act as a focus for the establishment of thickets in grassland; these thickets being the units of reforestation.

A comprehensive survey of the island termites was undertaken. Five species were collected belonging to four genera of the family *Termitidae*. These were *Macrotermes bellicosus* Smeathman, *M.natalensis* Haviland, *Microcerotermes nemoralis* Harris, *Odontotermes* (?) *zambesiensis* Sj., and *Amitermes evuncifer* Silv. The species composition is not unusual (W. Wilkinson, pers. comm.) The significant feature about the Lolui termites is their large numbers; a 50 x 50m. quadrat in the grassland of the north-west peninsula included ten inhabited termitaria of *Macrotermes bellicosus*, and two of *M.natalensis*; a similar quadrat taken at Chobi only included two termitaria, one of which was uninhabited, the other containing *M.bellicosus*. The numbers of termites on Lolui provide some indication of the abundance of primary production available to heterotrophs. It may be also taken to indicate that much of this primary production is not utilised by hippopotamus, monkeys or other grazing herbivores. It is suggestive of the fact that the ecosystem is under- rather than over-exploited, and would be capable of supporting other heterotrophs, possibly diurnal grazing antelope.

The origin of the grassland.

The extensive grasslands of Lolui Island appear to have arisen due to a break in the seral stages of succession following the evacuation of the island. Thomas (1941) suggests that the grassland phase is directly associated with soil infertility rather than directly with intensive settlement. This author does, however, record regeneration of woody vegetation on the Sese Islands, but says that it is slow except in association with termite mounds. It is not clear from his account where the mounds were located in relation to the soil types he mentions, but the red colour suggests that they are probably in the areas of yellow-red ferralitic soils. On Lolui since the evacuation of the human population, the reforestation that has taken place has tended to be more extensive in the sandy soils rather than the heavier yellow-red soils of the central plateau, which for the main part carries a grassland cover (c.f. Fig. 3).

The number of grass species in the main grasslands is low and dominants are limited to four species, *Hyparrhenia dissoluta*, *Andropogon dummeri*, *Loudetia kagerensis* and *Eragrostis blepharoglumis*. Snowden (1953) records these grasses from the Uganda mainland as grasses of specialised habitats within the forest zone. In tree species this zone corresponds closely to the forests of Lolui Island. When uninhabited or sparsely settled it is likely that Lolui was densely covered with forest, since neither proximity to the lake margin nor rocky substrate appear to limit forest formation (c.f. Plate 7).

Clearance of the forest for agriculture and subsequent fallowing would therefore result in secondary succession back to forest which in the early stages would involve grass species. The grass species involved in colonisation of the fallow land were apparently not the grasses of the forest floor, but rather those of specialised habitats such as shallow soils and exposed rock outcroops. Other grasses were not involved since they were not represented in the original island vegetation.

In areas of relic forest, especially with rocky substrate, which was presumably never at any time cleared for agriculture, several grasses occur which are for the most part limited to evergreen forest, such as *Pseudechinolaena polystachya*, *Panicum brevifolium*, *Oplismenus hirtellus*, and *Setaria aequalis*. These species are not found in the forest regrowths, and provide some indication of which areas are relic forest, and also the rate of reforestation.

The origin of the thickets.

Analysis of the species of tree and shrub found in the thickets shows that apparently without exception all species of woody vegetation have edible fruits. In the relic forest there are species with other modes of seed dispersal, but these species are not represented in thicket growth; examples are *Markhamia platycalyx*, which has wind-dispersed, winged seeds, *Albizia zygia*, *Baikiaea insignis minor* and *Mucuna* sp. which have explosive pods. There are likely to be others since the forest list in incomplete.

After the evacuation of the island, the pressure of the human population on other animals was removed and the monkeys were no longer restricted to the forest areas. Their day-ranging habits, which will be described in more detail in the appropriate section, include frequent expeditions into the grassland after the first feeding of the day in forest and thicket has terminated. Much sitting and "looking-out" on rocks and termite mounds is observed (Plate 11).

Plate 11. Beginning of a grassland expedition. A juvenile male sits on a termite mound looking round. An adult female approaches the mound through the grass.

Examination of any rock or termite mound within a group's territorial boundaries reveals many seeds in monkey droppings and many unfleshed seeds. Where grinding hollows were located on the top of a flat rock, these were frequently filled to the level of the surface of the rock with faecal remains which were almost exclusively the seeds of monkey food species. Droppings were collected and the seeds extracted, dried, sorted and weighed. The results are indicated in Table 7.

These seeds may either by washed off the rocks or mounds to the base, or actually into the tunnels of broken and abandoned termite mounds. They then tend to germinate. From field observation, the most frequent sites for the establishment of thickets are rocks and termite mounds; the least favourable site being the open grassland.

The species which are found most frequently as single individuals are _Saba florida_ and _Vitex fischeri_. Both form a dense cover which eliminates grass by shading. _Vitex_, even as an old tree carries foliage almost to ground level. _Saba_ has a dense foliage which gives complete cover when fully established. Once established, monkeys visit the trees or _Saba_ thickets for fruit or for shade and more species are soon found in association. _Harungana madagascariensis_ seedlings (Plate 12) are generally numerous and grow close to the edge of the canopy and extend the low cover into the grassland. _Garcinia huillensis_ and _Pachystela brevipes_ seedlings are found under the canopy and become established there.

TABLE 7

Analysis of monkey faeces for May 1963 and April-May 1964.

Species	May 1963 No.	May 1963 Dry weight (g)	April-May 1964 No.	April-May 1964 Dry weight (g)
Saba florida	37	49.1	48	58.2
Harungana madagascariensis	63	1.2	18	.4
Vitex fischeri	30	20.55	3	1.7
Popowia buchananii	20	4.0	-	-
Uvaria virens	8	1.6	1	.1
?Canthium vulgare	22	1.4	-	-
?Alchornea cordifolia	12	0.2	-	-
Residue Fibrous matter, plant remains insect remains*, sand.		37.3		19.56
Total		115 .35		79.96
Ratio, seeds:residue	1:0.49		1:0.32	

* Insect remains absent from the 1964 sample.

(Adapted from Jackson & Gartlan, 1965).

Plate 12. *Ficus* sp. sapling established in cleft between two rocks in grassland. Shrub at base is *Harungana madagascariensis*, which is also prominent in the low-cover in the background.

Plate 13. Termite mound in grassland. The spiky grass actually on the mound and immediately around the base is Eragrostis blepharoglumis. The grass in the foreground is Loudetia kagerensis. The different species show the different microclimate in the vicinity of termitaria permitting the establishment of a thicket focus.

Eragrostis blepharoglumis is commonly found all the way round thickets, and this is probably due to an increase in moisture caused by the presence of the thicket. However, as it is also commonly found round termite mounds (Plate 13) in the absence of overhead vegetation, it seems that in the latter case the termite mound offers a different microclimate, possibly in respect of improved drainage or soil brought to the surface through the layer of quartzite gravel which covers much of the lower slopes. This factor may be important in the germination of seeds left there by the monkeys, and in the eventual growth of thicket vegetation around this focus.

Saba florida is a constant member of thicket communities and forms a dense tangle of liane-like stems within the thickets. At the edges of the thickets Saba sends out long horizontal "pseudostolons" into the grasslands or surrounding vegetation, despite burning back; these runners aid in the extension of the thickets by smothering the grasses. Saba, although often damaged by grass fires, is seldom destroyed. Eventually, thickets in close proximity are joined together by Saba community, in which appear species which are more susceptible to fire damage. Canarium seedlings and saplings are often found within the Saba cover and many Canarium dominated clumps are apparently initiated in this manner. A typical Saba plant is shown in Plate 14.

Other plants besides Vitex and Saba initiate clump vegetation and Popowia is often found in the more rocky terrain near the forest fringes. Alchornea cordifolia is not uncommon, especially

Plate 14. Typical Saba florida plant overgrowing rock. Note the thin, liane-like pseudostolons and the abundance of fruits.

near the lake shores and may have *Ipomea cairica* climbing over it. *Morinda lucida* has been observed as a bush in open grassland.

The distribution of thickets and their relationship to the relic and fringing forests can be clearly seen in Fig. 3, which was redrawn from aerial photographs. The monkey population, as has been described, is not subject to predation pressures of any kind, and in this particularly rich environment seems to be reproducing remarkably quickly; in consequence there is some pressure on resources, particularly the fruit-bearing woody vegetation. The thickets, therefore, in offering a food supply that is both rich and unusually concentrated, are the main factor resulting in the frequent occurrence of several behaviour patterns, especially those concerned with the demarcation and defence of territory.

Paucity of plant and animal species distribution on Lolui.

It was earlier stated that Lolui Island most clearly corresponds in floral composition to the forest of the mainland designated moist semi-deciduous forest by Langdale-Brown, Osmaston and Wilson (1964), and is characterised by *Chlorophora excelsa*, *Albizia zygia*, *Antiaris toxicaria* *Baikiaea insignis*, *Canarium schweinfurthii*, *Maesopsis eminii* and *Ficus* spp. These species all occur in the relic forest of the island, and yet the absence of species other than the common forest constituents in the flora and the remarkably few species represented in the fauna, needs explanation.

One of the most striking absences from the flora is that of epiphytes and ferns. The Sese Islands are reported to be rich in species of these groups, whereas no epiphytic orchids were seen on Lolui throughout the entire study period, and only four common ferns were discovered. Palms are also strikingly absent; both Raphia monbuttorum and Phoenix reclinata are reported from lakeside forest of the Sese Islands, but are not found on Lolui. Uapaca guineensis, Piptadeniastrum buchananii, and Musanga crepidiodes all appear to be missing or rare, although widespread in Mengo and the Sese Islands. Elsewhere in Uganda, however, Piptadeniastrum and Uapaca are often felled in areas of cultivation because of serious root competition.

There are few climbers apart from the woody lianes. Culcasia scandens, Piper guineense and Basella alba, found in the Sese Islands are not recorded on Lolui, nor are the forest grasses Leptaspis cochleata and Streptogyne gerontogaea. The weed flora is also small when compared with the mainland, and although Ageratum conyzoides, Laggera alata and Senecio abyssinicus have been recorded, the common weeds of South American origin such as Acanthospermum hispidum, Tridax procumbens and Synedrella nodiflora are apparently absent. Also missing from the island flora are the common grasses such as Rhynchelytrum repens, Pennisteum polystachyon, Rottboellia exaltata and Setaria pallide-fusca.

Lolui was probably never an entirely homogeneous habitat: areas in the southern promontory unsuitable for cultivation are also probably unsuitable for forest growth. At the final isolation of the island, the island probably supported a mixed fauna; species of rocky habitats and animals characteristic of forest.

The clearing of the forest during the lengthy period of human habitation would as has been noted, have resulted in a reduction in the number of species and the number of individuals of each species in the island ecosystem. Elimination would have been either directly by hunting, indirectly by habitat destruction, or thirdly by increasing competition in the relic forests. The reduction in species and individuals may have resulted in the elimination of predators by reducing available food below a minimum level.

It is impossibly to state which of the present mammal species are probable relics. The most likely are Procavia capensis and Genetta tigrina, both of which are unlikely to have been introduced by man, and both of which are not known to swim. Other forest species could have been introduced at a later date, either through their own efforts; Naja melanoleuca is a capable swimmer, Limnotragus is known to travel on floating papyrus islands in Lake Victoria, and C.aethiops has been observed swimming in the Kavirondo Gulf, not far from Lolui, by Haddow (pers. comm.); Hall (pers. comm.) has observed individuals diving and swimming in Lake Kariba, and van Lawick (pers. comm.) has observed them "bathing" on Lolui Island itself. Monkeys are also likely to have been introduced by man as pets.

In an area of 11 square miles of undisturbed forest, thicket and grassland, one would have expected a much wider species composition. Species such as Cercopithecus ascanius, the redtail monkey, which occurs on the Sese Islands and islands to the north-west on Lolui; mongooses, Ichneumia spp., bush pig, Potamochoerus porcus, duikers, Cephalophus spp., are all conspicuously absent although all are known to occur on the islands of Lake Victoria.

There is no doubt that the island is now capable of supporting many of these forest species, especially those of the forest floor which would not compete with the monkey population, and also diurnal grazers such as Adenota kob, or Aepyceros melampus, the impala. The monkey population of almost 2,500 individuals could certainly support leopard, especially if the diet were to be supplemented by other species.

The present pattern of mammalian species composition therefore represents a population which survived severe and prolonged ecological deprivation, and which has now recovered and is expanding. It is also likely that invasion by species capable of movement across the lake barrier has taken place. But the mammal species composition is unbalanced, as is the floral composition, and lacks a sufficient number of sufficiently diverse species capable of dealing efficiently with the seral stages of ecological succession.

THE POPULATION STRUCTURE OF VERVET MONKEYS.

Population density

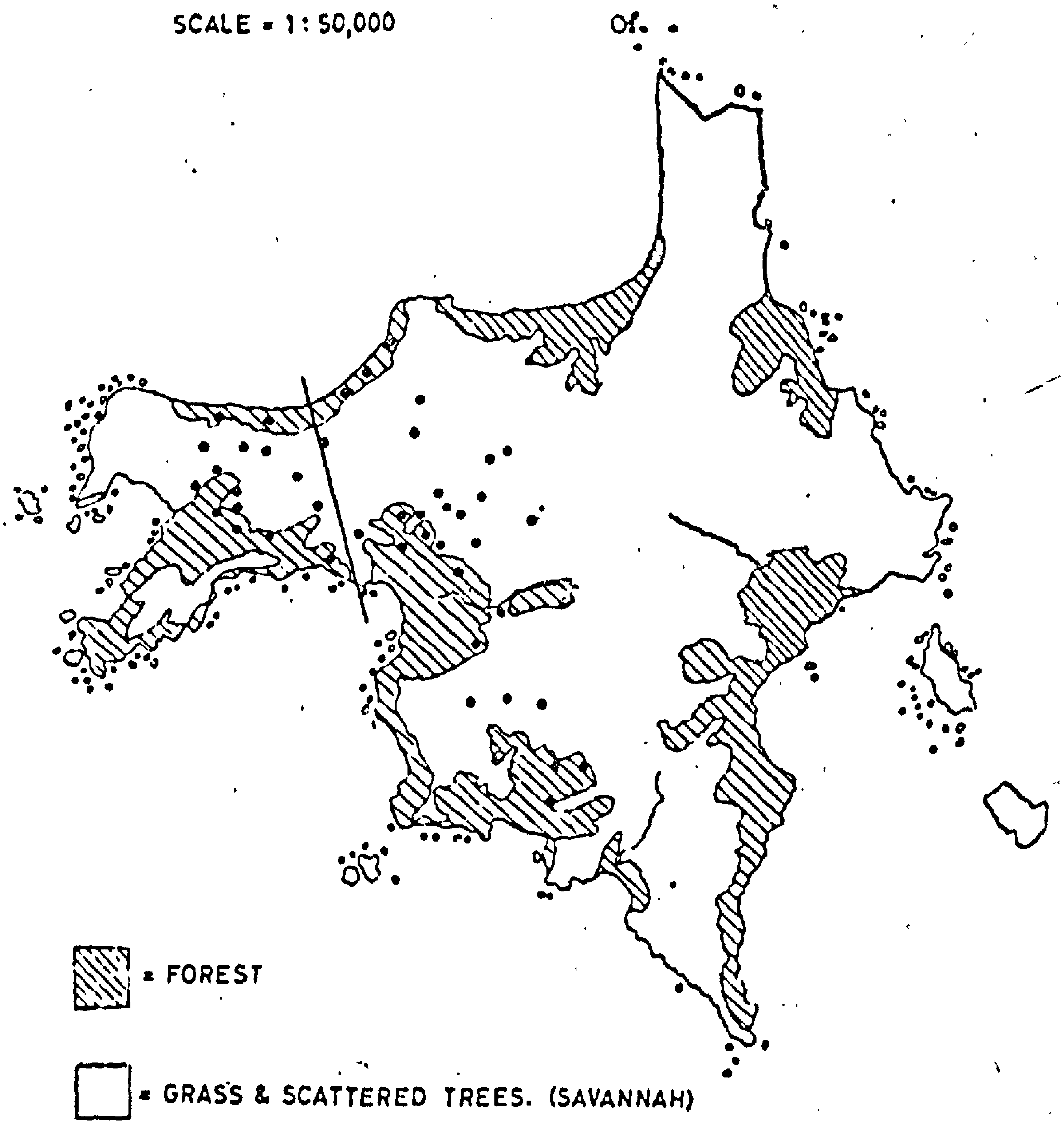
An initial estimate of the size of the monkey population of Lolui Island was based on data obtained during the joint survey with Professor K.R.L. Hall between 23rd April and 21st May 1963. The results were summarised by Hall and Gartlan (1965). Each worker spent about 240 hours in the observation and surveying of groups. A total of forty six groups was counted (Fig. 7) of which a complete age-sex analysis was possible on eighteen. These forty six groups were distributed throughout the western half of the island. At this stage of the survey, it must be pointed out, the concept of subadult was not used, and those animals which would later have been classified in this category were considered either as adult or juvenile females. This was also the case with the detailed survey of the north-west promontory which was carried out in June 1963.

The first estimate of the population density of Lolui was based on the total number of sightings of groups during the study period (89) and the fact that the survey covered only approximately two thirds of the 10.6 square miles of the island. It was estimated from these data that the island supported some 134 monkey groups. The mean size of the sample of 46 was calculated as 12, and it was therefore concluded that the island supported a population of some 1600 monkeys. In the light of later, more detailed information this can be seen to be an underestimate.

Later calculation of the population density were based on a

Fig. 7

(Redrawn from Hall & Gartlan, 1965)



—Lolui Island, showing main vegetation areas and locations of the 46 groups studied.

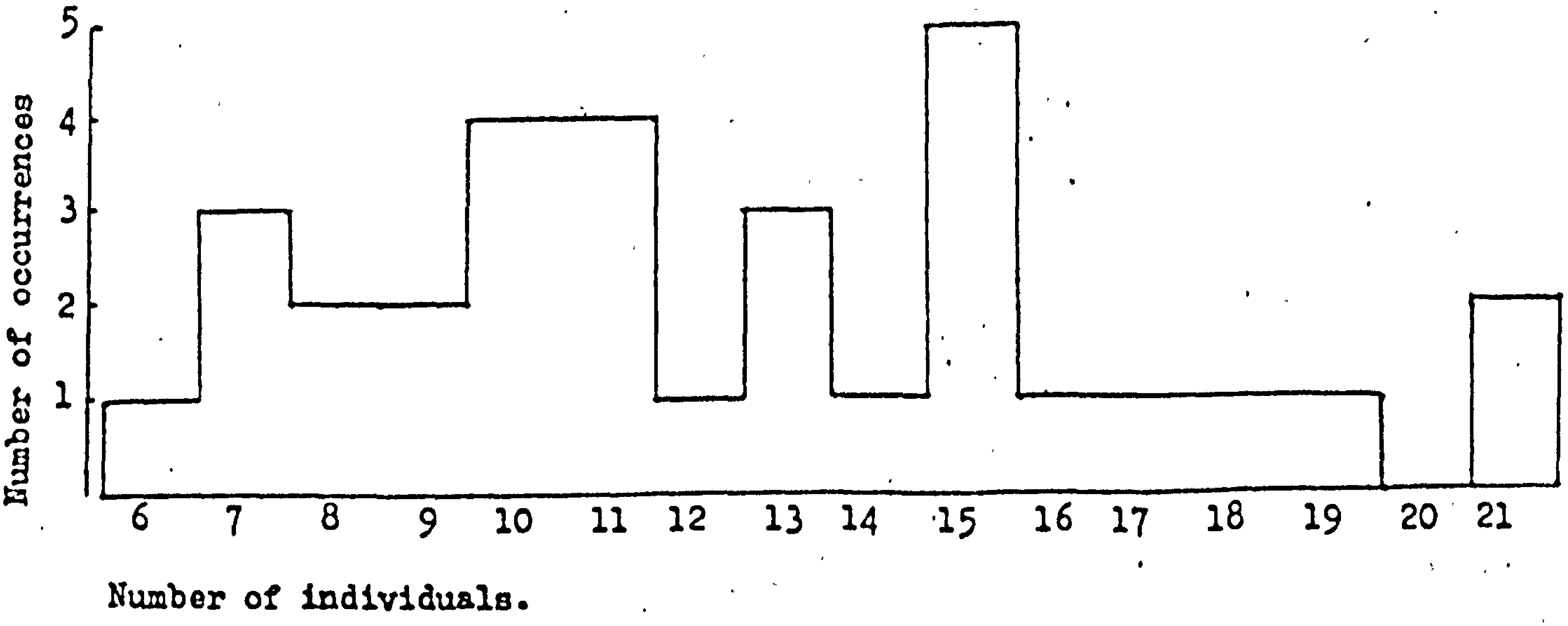
thorough and detailed survey of the thirty-two groups living in the north-west promontory. The area is indicated on Fig. 7. This analysis was carried out during the second study period between 4th June and 2nd July 1963, so allowing the minimum time for alterations in age-sex structure, although some differences were to be expected due mainly to the birth of infants during the intervening period.

A total number of thirty-two groups inhabited the north-west promontory of the island. Fifteen of these were included in the original sample of forty-six. The total number of individuals living in these groups was 397, with the sizes of groups as indicated in Fig. 8. An analysis of the proportional area occupied by these groups relative to the total area of the island was carried out by cutting a photocopy of an aerial photograph of the island into the two respective parts and comparing their weights. The results indicate that the area occupied by the thirty-two groups constitutes 16.6% of the total area of the island. On this basis, the estimate of the total population is calculated as 2382 individuals. The total area of Lolui is 10.6 square miles, giving an approximate density per square mile of 225 individuals.

The population density is particularly high, especially in view of the fact that forest and thicket areas were not the only ones considered in the calculations. The only other estimates of population density for such a relatively closed ecosystem are those given by Carpenter (1934) for the howler monkeys,

Fig. 8

Numerical sizes of 32 groups of the north-west promontory, Lolui Island.



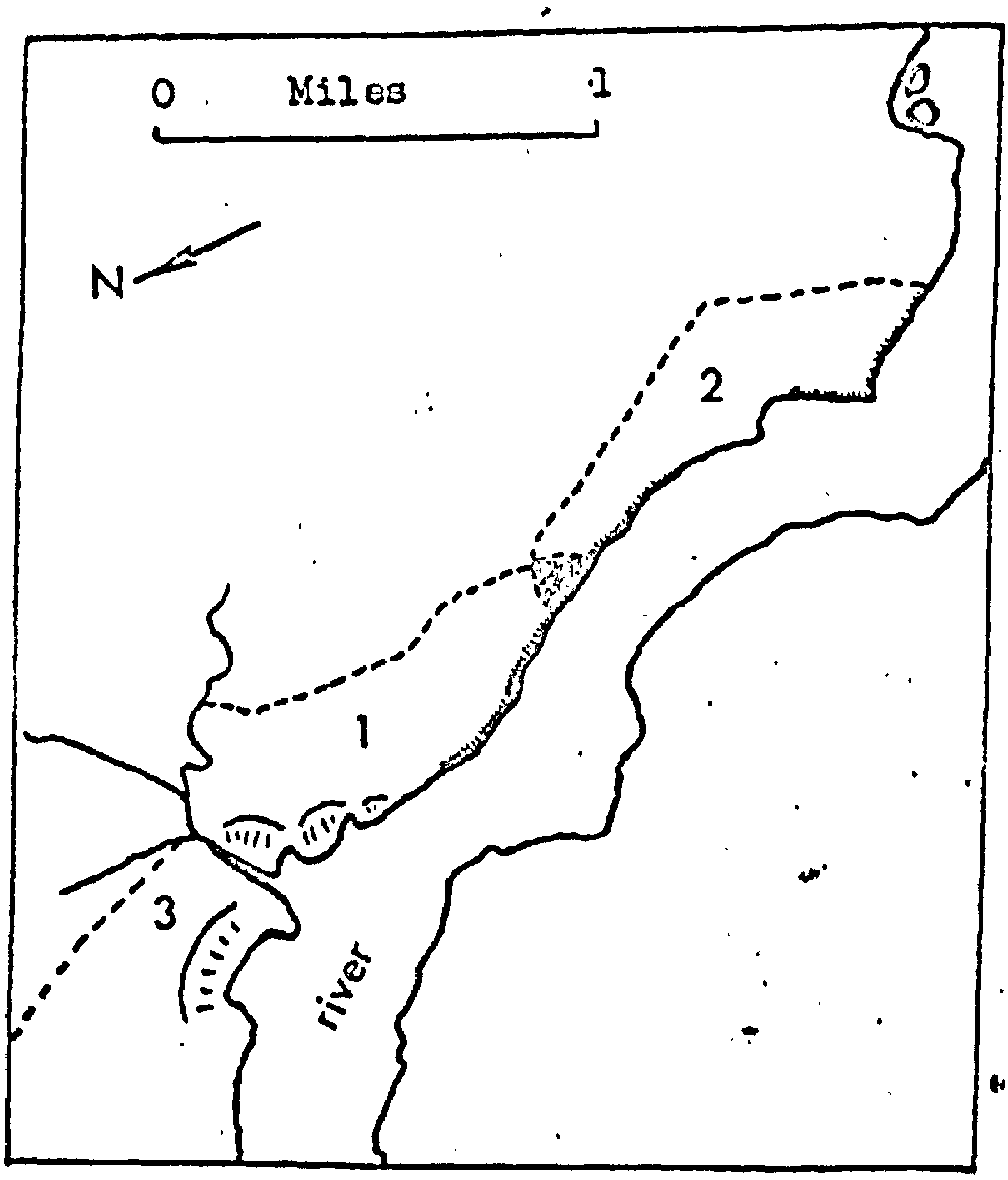
Aloutta palliata of Barro Colorado Island, Panama, and by Sade and Hildreth (1965) for an introduced population of Cercopithecus aethiops sabaeus on St. Kitts, West Indies. The figures per square mile calculated from Carpenter's (1934) data are 64.7 for 1932, and 81.6 for 1933. This population is apparently subject to considerable fluctuations, and figures calculated from Carpenter's chapter in DeVore (ed.) (1965) give figures of 46.2, 39.8 and 135.8 for 1935, 1951 and 1959 respectively. Barro Colorado, it should be noted, is almost completely covered with tropical rain forest which is the typical habitat of the species. Sade and Hildreth (1965) give figures indicating a population density of 71 per square mile for C.a.sabaeus artificially introduced onto St. Kitts in the West Indies.

There are no estimates of the normal population density of C.a.pygerythrus in the literature. C.K. Brain (pers. comm.) who has studied the subspecies both in the wild and in captivity in Rhodesia and South Africa, suggests that the Lolui density "far exceeds" any he has ever encountered in either of the two countries mentioned.

Evidence from the study of the population at Chobit indicated a much lower population density there. This population is confined to a narrow strip of riverine vegetation along the banks of the Nile. The habitat is both impoverished and deteriorating due principally to overgrazing by hippopotamus and elephant (Appendix 2). Three groups inhabited the strip of riverine vegetation shown in Fig. 9. Much of the daytime foraging and feeding took place

Fig. 9

Home range areas of three C.aethiops groups at Chobi, N.Uganda.



◠ = Erosion areas

⁀ = Riverine strip vegetation

○ = Areas of home range overlap

in the grasslands where Acacia sieberiana and Terminalia glaucescens occurred, the leaves of which formed a major part of the monkey diet. The density of this population was based on the furthermost day ranges used by the groups. These are indicated in Fig. 9. The numbers in each group were 25, 13, and 16. The area of range was .94 square miles, giving an approximate density of 57 per square mile. This difference in population density between Lolui and Chobi is considered to be one of the major factors accounting for the difference in social behaviour between the two populations. On Lolui, for example, territories were marked, well-defined and defended by several behaviour patterns, whereas at Chobi no such behaviour was observed and home ranges overlapped (Fig. 9.) There was also occasional mixing of groups at Chobi.

Age and sex distribution.

The age and sex distribution of the eighteen groups that it was possible to count and sex completely in the original sample of forty-six are shown in Table 8. The comparable data for the thirty-two groups counted in June are given in Table 9. It was stated (Hall and Gartlan, 1965) that the most reliable group counts were those obtained on first contacting the group as all members tended to come into full view and watch the observers. That the statement was well founded can be seen from the fact that the mean group size of 12 obtained from the first survey compared

TABLE 8

Analysis by age and sex classes of 18 groups of vervet monkeys on Lolui Island.

Adults		Juvs.		Infants		Total adults and juvs.		Total		Total
♂	♀	♂	♀	2	1	♂	♀	Adults	Immat.	in Gp.
6	8	3	2	-	1	9	10	14	6	20
4	5	4	4	-	2	8	9	9	10	19
4	5	4	3	2	-	8	8	9	9	18
3	4	3	2	2	1	6	6	7	8	15
2	4	3	3	2	-	5	7	6	8	14
4	4	2	3	-	1	6	7	8	6	14
3*	5	2	1	1	1	5	6	8	5	13
4	5	3	1	-	-	7	6	9	4	13
2*[1]	5	4	2	-	-	6	7	7	6	13
2	3	3	1	2	1	5	4	5	7	12
2	4	3	1	-	2	5	5	6	6	12
2	3	3	1	2	1	5	4	5	7	12
4*	4	1	2	-	-	5	6	8	3	11
2	4	1	3	1	-	3	7	6	5	11
2	4	1	2	-	1	3	6	6	4	10
3*	2	1	2	-	-	4	4	5	3	8
2	3	1	1	-	-	3	4	5	2	7
2*	2	1	1	-	1	3	3	4	3	7

cont/

TABLE 8 (cont.)

Adults		Juvs.		Infants		Total adults and juvs.		Adults	Total Immat.	Total in Gp.
♂	♀	♂	♀	2	1	♂	♀			
				Totals						
53	74	43	35	12	12	96	109	127	102	229
				Sex ratios						
1	1.4	1	0.8			1	1.1			

* Included in the detailed survey of the north-west peninsula, (Table 9).

1 Group showing a change in constitution between the two surveys.

TABLE 9

Analysis by age and sex classes of 32 groups of vervet monkeys from the north-west peninsula of Lolui Island.

Gp.	Adults		Juvs.		Infants		Total adults and juvs.		Total Adults	Total Immat.	Total in Gp.
No.	♂	♀	♂	♀	1	2	♂	♀			
1	3	6	1	5	1	-	4	11	9	7	16
2	4	5	2	2	-	1	6	7	9	5	14
3	3	5	2	1	1	1	5	6	8	5	13
4	3	5	4	2	1	-	7	7	8	7	15
5	4	4	1	2	-	-	5	6	8	3	11
6	3	2	1	2	-	-	4	4	5	3	8
7	2	2	1	1	1	-	3	3	4	3	7
8	2	4	2	1	1	-	4	5	6	4	10
9	2	2	1	2	-	-	3	4	4	3	7
10	6	7	2	2	3	1	8	9	13	8	21
11	2	3	-	1	1	2	2	4	5	4	9
12	3	4	2	1	-	-	5	5	7	3	10
13	3	2	1	2	-	-	4	4	5	3	8
14	4	6	3	4	-	-	7	10	10	7	17
15	2	4	2	1	1	-	4	5	6	4	10
16	2	2	1	1	-	-	3	3	4	2	6
17	3	2	1	3	-	-	4	5	5	4	9
18	2	4	2	2	1	-	4	6	6	5	11
19	2	2	2	1	-	-	4	3	4	3	7
20	4	5	2	3	2	2	6	8	9	9	18

cont/

TABLE 9 (cont.)

Gp.	Adults		Juvs.		Infants		Total adults and juvs.		Total Adults	Total Immt.	Total in Gp.
No.	♂	♀	♂	♀	1	2	♂	♀			
21	3	4	2	1	2	-	5	5	7	5	12
22	2	3	2	2	-	2	4	5	5	6	11
23	2	4	2	1	2	-	4	5	6	5	11
24	3	4	3	3	1	1	6	7	7	8	15
25	3	4	2	2	2	-	5	6	7	6	13
26	4	5	3	2	-	1	7	7	9	6	15
27	4	4	2	2	1	2	6	6	8	7	15
28	5	6	5	3	-	-	10	9	11	8	19
29	2	4	1	1	1	1	3	5	6	4	10
30	2	4	3	2	1	1	5	6	6	7	13
31	5	7	4	4	-	1	9	11	12	9	21
32	3	5	3	2	-	2	6	7	8	7	15
Totals											
	97	130	65	64	23	18	162	194	227	170	397
Ratios											
	1 :1.34		1:0.98				1:1.19				

with that of 12.4 from the survey of the thirty-two groups of the north-west promontory. Part of the difference obtained is due to the fact that as the second survey took place later, the birth season was more advanced and there were more infants in groups. The ratio of infant ones to the total population of the 18 groups counted initially was 1:19, whereas in June on the north-west peninsula, the ratio was 1:17. The sex ratio of adult males to adult females was 1:1.4 in the initial survey, and 1:1.34 in the survey of 32 groups, giving a mean ratio of 1:1.37.

The reliability of the first joint survey was assessed by means of a Mann-Whitney U Test (Siegel, 1956, p 116), comparing the distribution of groups obtained with the figures obtained during the complete count of the 32 groups of the north-west peninsula. This statistical test is nonparametric, making no assumptions about the normality of the population, and assesses the probability of the samples in question having been drawn from the same population.

Five of the groups were included in both samples, and for the purposes of this calculation these groups (3 - 7, Table 9) were included in the first sample and excluded from the second. The null hypothesis tested was that both samples have the same distribution. As no direction of difference was predicted, the test is two-tailed. As many group sizes were the same, a correction for ties was incorporated into the calculations.

The value of z was calculated as -.70. Under the table of probabilities associated with values as extreme as observed values of z in the normal distribution, the probability of such an occurrence was observed to be .2420 for a one-tailed test, or .4840 for a two-tailed test. A value of 2.33 would be required for the rejection of the null hypothesis at the .01 level of confidence. The null hypothesis is therefore retained.

The conclusion to be drawn from the foregoing calculation is that both samples have similar distributions. This vindicates the reliability of the initial joint survey, and it is proposed to utilise the results of both surveys in the assessment of the population parameters.

The maximum group size was 21 and the minimum 6 individuals. The range was 16 with a mean group size of 12.3. There are reports of group sizes of the species group throughout the distribution range. Hall (1965) gives a mean of 11 (N = 10) for groups of this species counted in the Murchison Falls National Park, in northern Uganda. A count of three groups at Chobi gave the previously mentioned figures of 25, 16 and 13. Hall worked at Chobi and it is possible that one of these three groups was counted by him and included in his data. Summarising the data from Uganda, it may be stated that the range of group sizes is from 4 to 25 with a mean of 14.5 animals per group.

R.C. Wingfield (pers. comm.) gives a range of from 7 to 51 for groups in the Victoria Falls and Lake Kariba areas (N = 9). T.S. Jones (pers. comm.) says that the group size of the species in the mangrove swamps near the mouth of the Senegal River varies between 20 and 40.C.H.B. Grant (quoted Elliot, 1913) says that in the Hlatwa district of Zululand the species is commonly seen in parties of from 6 to 12, and in the Cape Colony in groups of "six or more". C.K. Brain (pers. comm.) says that groups of up to 50 individuals "are not infrequent" in Rhodesia and South Africa. Two groups counted in the Nairobi National Park by the author were 15 and 18; a group counted in the Masai Amboseli Reserve comprised 23 individuals. Starck and Frick (1958) give a range of from 20 to 50 "as a rule" for the size of groups in the eastern part of Ethiopia. It is also of interest to note that Sade and Hildreth (1965) record a range of from 5 to 40 for the population of *C.a. sabaeus* for the exotic population on St. Kitts, West Indies.

The trend of these data indicates that there is less variability in group sizes in the East African sample. As far as is known there is no record of a group size of over 25 from this region. To the south and the north records of over 25 individuals per group are not uncommon. The trend seems to indicate an increased variability of group size in climatically more variable areas. Variability in this sense means areas subject to severe dry seasons or other climatic features which might act as limiting factors in the population dispersion. The possible adaptive significance of this will be discussed in the appropriate section, but it is clear that much more evidence about the variability of group size is necessary before definitive conclusions can be drawn. Present evidence is merely suggestive.

The mean sex ratio of adult males to adult females for both samples of the Lolui population was 1:1.37. Part of this difference must be accounted for by different rates of maturation; there was no evidence of differential mortality, and an equal sex ratio at birth is assumed. There are, as has been pointed out, no predators on the monkey population of Lolui.

In a population which has been established for many years, which is replenished by regular breeding and in which the different rates of maturation are constant for each sex, it seems reasonable to assume that differences in sex ratio dependent on differential maturation rates will also remain relatively constant. The ratio of juvenile males to juvenile females calculated for the two samples was 1:.89, and as both sexes leave the infant two stage at the same age, but enter the adult category differentially, the observed difference may be taken as indicative of the difference due to differential maturation rates. For every juvenile male in the samples, .11 females had reached sexual maturity. On this basis the observed sex ratios of adults can be compared with the expected frequencies derived from the hypothesis that for every adult male there should be 1.11 adult females. The significance of the differences between observed and expected frequencies was assessed by means of a Chi-square test (Siegel, 1956, p42). The total number of observed adult males in the two samples was 133, which would lead to an expected frequency of 147 adult females. In fact a total of 187 adult females was observed. The value of Chi-square calculated from these data was 10.88, which enables the null hypothesis to be rejected at over the .001 level of confidence. The conclusion is permitted that after the juvenile stage, males are under-represented in social groups. No all-male groups were observed; it must therefore be assumed that the observed difference is due to males becoming either temporary or permanent social isolates. Field evidence suggests that in the majority of cases, isolation is probably temporary.

The sex ratio of adult males to adult females on Lolui was, as has been mentioned, 1:1.37 (N = 45). At Chobi the figures for the three groups counted by the author were 1:2, 1:1.5 and 1:1.7, giving a mean value of 1:1.73 for the three groups. The ratios of the two groups counted in the Nairobi National Park were 1:1.66 and 1:1.25, giving a mean value of 1:1.45. A group in the Masai Amboseli Reserve had a ratio of 1:1.33.

R.C. Wingfield (pers. comm.) gives ratios of 1:6, 1:8, 1:7 and 1:2 for the only Rhodesian groups he was able to count completely. Information about the sex ratio of this species group is less frequent than that on group size, but from this evidence, and from what it is possible to infer from anecdotal and incidental information about troops being led by "single old males" (Lydekker, 1894) suggest that the sex ratio may be biased in favour of adult females in certain areas. From the definite evidence recorded above, it is apparent that East African groups tend to have a rather high sex ratio, varying between unity and a maximum of 1:2. Only one of the East African groups has a ratio as low as 1:2, and only one of the four Rhodesian groups was as high as this; the mean of the four groups being 1:5.75. The conclusion may be drawn that in this species group increased variability in group size, which occurs in areas with increased climatic variability, may be accompanied by a reduction of males in groups. The subspecies which show these changes, C.a.pygerythrus and C.a.cynosurus are those which extend furthest south in the distribution range, and which show a tendency towards increased male dimorphism in the climatically more variable areas; the more frequent occurrence of the red-brown bar under the base of the tail (Tables1-3) being a case in point. No information is yet available about other possible aspects of increased sexual dimorphism, such as in dentition or weight and size.

The conclusion that can be drawn tentatively from the information is that the species group is capable of some degree of social adjustment under ecological conditions which demand it. This approximates to the position in the arid country primates of Ethiopia, where Erythrocebus patas, Theropithecus gelada and Papio hamadryas have all evolved the one-male-group social structure in response to ecologically impoverished and climatically variable conditions.

Evidence from captive populations supports the adjustment hypothesis. C.aethiops is notoriously difficulty to keep in captivity because of the amount of aggression normally encountered in captive groups. C.K. Brain (Gartlan and Brain, in press) had considerable difficulty in setting up captive groups with an age-sex ratio similar to that of small wild groups. Part of the reason seems to have been the small area in which the groups were kept, a cage 8' x 13' x 15' being used. Yet M. Lyall-Watson (pers. comm.) successfully kept 57 animals, of which 30 were adult males in a large aviary containing a rock pile 20' high in the Johannesburg Zoo, and noted very little aggression. A small captive group of two adult males, four adult females and one juvenile male kept in a wire cage 12' x 8' x 9' in Uganda showed one aggressive incident per 12.4 minutes during five hours of observation*.

The same groups, minus one adult female which died in transit to England, was kept at Bristol in a cage 20' x 10' x 8', at a constant temperature of 75°F, and showed only one aggressive incident per 28.6 minutes over 20 hours of observation. The female which died was ailing during most of the initial investigation in Uganda and was not involved in any aggressive incidents. Her disappearance from the group is unlikely to

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*In this study of a captive group, "aggressive incident" included all aggressive behaviour from a mild threat-face to chasing and biting. But supplanting was excluded. The observations were not made at feeding time, when aggression was much more common. There was, however, generally some food available in the cage and this was a common source of aggression, 42% of the incidents in the Uganda captive study being so caused, and 37.4% in the Bristol study of the same group.

have been an important factor in reducing aggression, apart from increasing available space for other members of the group.

Further experiments need to be carried out on this problem, especially to investigate whether social changes resulting from captive conditions are reversible; in other words, if social adjustment to a one-male-group through increased aggression may be reversed and a multi-male group permitted if the group be transferred from a small cage to a large compound.

Stability of groups.

The observed variance of group size in C.aethiops in different parts of the distribution range raises the problem of the stability of social groups. In many field studies of primate social organisation such stability has been assumed in the lack of definite evidence for or against. In other studies the concept of "group" in the sense of a discrete and stable number of individuals characterised by boundaries of the type and frequency of social interactions, seems not to apply. This is evidently the case with the chimpanzee (Goodall, 1965; V. and F. Reynolds, 1965). P. Aldrich-Blake (pers. comm.) has also noted a lack of stability in groupings of C.mitis in the Budongo Forest. Hall (pers. comm.) noted the complete breakdown of the normal social structure of a baboon group trapped on an island by the rising waters of Lake Kariba.

The social group is presumably that unit permitting the most efficient dispersal in the environment, whilst at the same time affording maximum benefits to the individuals forming the group.

It is in the majority of cases structured appropriately to ecological conditions rather than being characteristic of the species concerned. The social structure of forest dwelling rhesus, for example (Jay, pers. comm.) is more similar to that of other forest-dwelling primates than to that of urban rhesus. One of the main advantages of a stable social group, especially when considered in conjunction with the prolonged immaturity characteristic of primates, is that a maximum knowledge of the behaviour and 'temperament' of other individuals is possible, and that opportunities to learn behaviour patterns appropriate to the ecological conditions of the habitat are maximised. It is likely that the particular pressures of conditions in the savanna and forest fringe, with a particular vulnerability to predation, would lead to social groups that were particularly stable. There is evidence, however, that social learning does not occur indiscriminately between group members. The role of the mother-infant bond is the propagation of new food habits in Macaca fuscata has already been demonstrated by Kawamura (1959). In an experiment in the laboratory at Bristol, which was unfortunately terminated prematurely by the destruction of the colony, it had been established that adult males failed to learn a simple bar-pressing task by observing other group members engaged in that activity. Two juvenile animals (one a young patas monkey) did however learn the task after only one trial spent in observing adult females, (not their mothers,) performing the bar-pressing task. The most rapid observational learning was demonstrated by an infant patas watching its mother performing the task. This infant reached the experimental criterion of 30 presses in a ten minute period, which had taken some adult females six half-hour sessions to reach. These data would seem to indicate that if modification of group social structure were to be necessitated by ecological or other conditions, the loss of adult males could be affected without altering the transmission of social traditions and the learning of behaviour patterns by infants.

It is difficult to obtain reliable information about the stability of groups without long-term studies. Marking of individuals is also desirable, although this was not attempted on Lolui. Of those groups which were included in both surveys on Lolui (Tables 8 and 9) only one showed any difference in social structure between the two counts (a period of two months) except for changes due either to births or maturation. This occurred in Group 4 (ninth in Table 8) which showed an increase from 2 to 3 adult males. More detailed information was obtained from Group 1, in which males were identified individually, throughout the study periods indicated in Table 10. All changes in this Table can be explained either by births or maturation except for those involving the adult male structure of the group, with the single exception of a subadult female which disappeared between 17.3.64. and 7.5.64. The total number of adult males only varied between three and four, and was the same at the beginning and end of the study, but during this time a total of

TABLE 10

Analysis of changes in composition of Group 1, Lolui Island, 5th June 1963 to 25th May 1964.

Individuals	Totals	Changes
(5.6.63 - 29.6.63)		
AM1, AM2, AM3	3AM	
AF1, AF2, AF3, AF4, AF5, AF6	6AF	
JM	1JM	
JF1, JF2, JF3, JF4, JF5	5JF	
I11	1I1	
Total	16	
(7.8.63 - 29.8.63)		
AM1, AM2, AM3, AM4	4AM	One more
AF1, AF2, AF3, AF4, AF5, AF6	6AF	No change
JM	1JM	No change
JF1, JF2, JF3, JF4, JF5	5JF	No change
I11, I12, I13, I14, I15	5I1	Four more
Total	21	
(9.10.63 - 27.10.63)		
AM1, AM3, AM4, AM5	4AM	One less, one joined
AF1, AF2, AF3, AF4, AF5, AF6	6AF	No change
JM	1JM	No change

cont/

TABLE 10 (cont.)

Individuals	Totals	Changes
JF1, JF2, JF3, JF4, JF5	5JF	No change
I11, I12, I13, I14, I15, I16	6I1	One more
Total	22	
(7.1.64 - 25.1.64)		
AM1, AM3, AM4, AM5	4AM	No change
AF1, AF2, AF3, AF4, AF5, AF6	6AF	No change
JF1, JF2, JF3	3SF	Three more
JM	1JM	No change
JF4, JF5	2JF	Three less
I11, I12, I13, I14, I15	5I2	Five more
I16	I11	Five less
Total	22	
(27.2.64 - 17.3.64)		
AM1, AM4, AM5	3AM	One less
AF1, AF2, AF3, AF4, AF5, AF6	6AF	No change
JF1, JF2, JF3	3SF	No change
JM	1JM	No change
JF4, JF5	2JF	No change
I11, I12, I13, I14, I15, I16	6I2	One more
Total	21	

cont/

TABLE 10 (cont.)

Individuals	Totals	Changes
(7.5.64 - 25.6.64)		
AM1, AM4, AM5	3AM	No change
AF1, AF2, AF3, AF4, AF5, AF6	6AF	No change
JF1, JF3	2SF	One less
JM	1JM	No change
JF4, JF5	2JF	No change
I11, I12, I13, I14, I15, I16	6I2	No change
I17	1I1	One more
Total	21	

five adult males was associated with the group, and only one remained with it through the entire study. This illustrates how misleading simple counting of individuals may be.

A survey of the number of adult males with the thirty-two groups of the north-west peninsula was carried out in February 1964 in order to obtain some information on the degree of change between groups shown by adult males. Simple counting was used although, as has been pointed out, this is likely to underestimate the total number of changes. The results are indicated in Table 11. The original figures for the 32 groups which were obtained in June 1963 are also included in this Table for reference.

The figures for groups 26 and 27 were not obtained in the February census because the groups had apparently left their old territories. These had been adjacent in a clump of relic forest at the edge of a rock escarpment on the south-western tip of the north-west peninsula. The area had been considerably disturbed by fishermen cutting tall straight saplings for the construction of huts and fish-drying frames. There was no indication where the groups had gone, but it was clear that they had not joined neighbouring groups, as the slight differences in male composition also indicates, and it seems possible that the entire groups evacuated the areas as groups.

Some of the increases observed in the number of adult males in groups must be accounted for by maturation, but the evidence from Group 1 also indicates both that changes do occur, and that

TABLE 11

Observed changes in adult male constitution of vervet groups on the north-west peninsula between June 1963 and February 1964.

Group	AMs in June '63	AMs in Feb.'64	Group	AMs in June '63	AMs in Feb. '64
1	3	3	17	3	3
2	4	4	18	2	3
3	3	4	19	2	3
4	3	2	20	4	4
5	4	5	21	3	3
6	3	3	22	2	2
7	2	2	23	2	2
8	2	3	24	3	3
9	2	2	25	3	4
10	6	4	26	4	n.o.
11	2	3	27	4	n.o.
12	3	3	28	5	4
13	3	3	29	2	2
14	4	4	30	2	3
15	2	3	31	5	4
16	2	2	32	3	4

they occur fairly freely.

The phenomenon of male interchange between social groups is not rare in recent primate literature, but it is to be expected that reports of the phenomenon will increase as further studies are completed in which individual animals are identified. Schaller (1965) records the changing of adult male mountain gorillas between groups; T.E. Rowell (pers. comm.) records the same phenomenon for baboons in Uganda; Hazama (1964) records the disappearance of over 20 "leading males" from the Arashiyama troops of Macaca fuscata between 1954 and 1956, and notes that in many cases the animals were not driven out but apparently left voluntarily.

On a priori grounds it is to be expected that there would be some interchange of genetic material between groups, as only through such a mechanism could the conspicuous homogeneity of a species such as C.aethiops be maintained. It is interesting, however that it occurred on Lolui where territorial behaviour was so pronounced, as of there were any limiting factor on the exchange of adult males between groups, one would have expected territorial behaviour to provide it. One instance of the failure of territorial behaviour to provide a functional breeding barrier between different groups was observed in Groups 1 and 8. AM2, a fully grown adult male of Group 1 left the group between 29th August 1963 and 9th October and joined neighbouring Group 8, with territorial boundaries adjacent to those of Group 1. It was not apparently chased out and was not marked by any scars when first observed in Group 8. When it was a member of Group 1 it was not involved in more aggressive incidents than were other adult males, as far as it was possible to tell. On joining Group 8 it was seen on three occasions chasing out members of Group 1 who had trespassed into Group 8's territory. It was observed on two further occasions trespassing back into his old territory, but on both occasions ran back to that of Group 8 on hearing members of Group 1 approaching.

The data shown in Table 11 on the changes in the adult male composition of groups were analysed by means of a Wilcoxon matched-pairs signed-ranks test (Siegel, 1956, p. 75), to determine the significance of changes observed between the two samples. For this test the figures obtained in each sample are matched into pairs, corresponding to the two counts of each group (Groups 27 and 27 being dropped from the analysis). The differences between the two counts (d_1) are then calculated and the sign inserted. Where there is no difference the pairs are dropped from the analysis. By inspection of the data shown in Table 11, it can be seen that there are 13 differences of 1 and 1 of 2. Three of the differences of 1 are negative, the rest are positive, and the difference of 2 is negative. These differences are then ranked and the ranks given the sign of their respective d_1. Siegel states that ties have a negligible effect on the statistic. The like-signed ranks are then added, and the smaller is considered as T. The obtained value of T was 35. The statistic z is then calculated using formula 5.5 (Siegel, p 79) using T, and the obtained value is -0.09. The probability of this occurrence for a two-tailed test is .9282. The difference between the two samples is not significant at the .05% level of confidence. Thus, although it is clear from the data presented in Table 11 that changes in the adult male composition of groups do occur, it is equally clear that the observed changes are small. In view of the detailed data obtained for Group 1, this is likely to be an artefact of the simple counting method which tends to underestimate changes.

In view of the discovery of the interchange of males between groups, and the observed variance of the adult male component of groups throughout the distribution range, it was decided to make an analysis of the patterns of social interaction within the group with the aim of attempting to establish the degree to which adult males were independent of groups. The subjective impression gained after several months of study was that the constant nucleus of a monkey group on Lolui Island was the adult female component, along with the infants and to some extent the juveniles and subadults. No adult female was ever observed either solitary or peripheral to groups, nor was any ever observed to change between groups, although a detailed census of changes in the adult female component of the population was not carried out. No adult female either left or joined Group 1 during the year of detailed study, although one subadult female did leave. And no difference in the adult female component of groups in the north-west peninsula that were counted twice was noted, although one male had joined Group 4 during the intervening period.

It was decided to investigate which age-sex categories of animals were habitually found away from other animals, if any, by studying two groups, Group 10 and Group 12 for three days each, noting every fifteen minutes which animals were more than 10 metres away from another animal. These observations were carried out between January 10th and 15th, 1964 inclusive, and the composition of the two groups was as follows,

Group 10. 6AM, 7AF, 2JF, 2JM, 3I1, 1I2.
Group 12. 3AM, 4AF, 1JF, 2JM, 2I2.

Observations were begun at 0645 hrs and continued through until 1900 hrs. The total number of incidents is shown in Table 12.

It was decided to test whether there was any significant difference in the ratio of incidents within each age-sex category between the two groups, this was to establish whether there was any difference between the two groups. If this was observed, it would indicate a degree of variability in this social pattern which would not justify combining the data from the two groups, and would need further explanation. The significance of the differences between the two groups was assessed by means of a Mann-Whitney U test (Siegel, loc. cit.). As it was the proportionality between the two groups and not the absolute values that were to be assessed, the test was calculated on the percentage of incidents in each age-sex category relative to the total scores of the group. These percentages were calculated as follows,

TABLE 12

Total number of incidents of an individual being more than 10m. from another individual; groups observed at intervals of 15 min.

Group	Date	Age-sex category of individual			
		AM	AF	JM	JF
10	10.1.1964	30	16	7	2
	11.1.1964	24	15	3	1
	12.1.1964	26	9	13	3
	Total	80	40	23	6
12	13.1.1964	13	6	5	3
	14.1.1964	11	8	12	2
	15.1.1964	12	6	11	6
	Total	36	20	28	11

	AM	AF	JM	JF
Group 10	54%	27%	15%	4%
Group 12	38%	21%	29%	12%

The value of U calculated from these data was 7. The test is two-tailed as no direction of difference is predicted. The probability of this occurrence is .442, which is not significant at the .05% level of confidence. The conclusion is permitted that the two groups could have been drawn from the same population in respect of their proportionality. It is possible therefore to combine the scores of both groups without distorting the patterns within groups.

The combined figures for the raw data of both groups give the following distribution,

AM	AF	JM	JF
116	60	51	17

The total number of animals in each age-sex category of the two groups are

AM	AF	JM	JF
9	11	4	3

Given these data it is possible to apply a Chi-square one-sample test (Siegel, loc. cit.) to determine whether the observed differences are distributed throughout the age-sex categories proportionally to the numbers in the categories. The percentages of animals in each age-sex category are

AM	AF	JM	JF
33%	41%	14%	11%

giving expected scores of 81 100 34 27

The value of Chi-square calculated from these data was 43.32. There are three degrees of freedom (k - 1) and the obtained value is significant at over the .001 level of confidence. The null hypothesis must therefore be rejected and it can be stated that the age-sex category to which an individual belongs has a significant influence on the probability of that animals being found more than ten metres away from another animal. This probability is high for adult males and low for adult females, thus emphasising the relative independence of adult males from groups, and the relative frequency with which adult females are found in close association with other animals. The same tendencies, although less strongly marked, are observed in juvenile animals.

Birth periodicity.

One of the most persistent controversies running through the literature on primate social organisation and behaviour has been the question of periodicity in mating. This stems directly from Zuckerman's (1932) hypothesis that in primates mating occurred continuously throughout the year and provided the motivational basis of the bonds uniting primates into social groups. Evidence from zoos and colonies has frequently been ambiguous, but recent reports of field studies of free-ranging primates have increasingly demonstrated restricted birth seasons, which by implication assumes a time of the year when copulation is either rare or none existent.

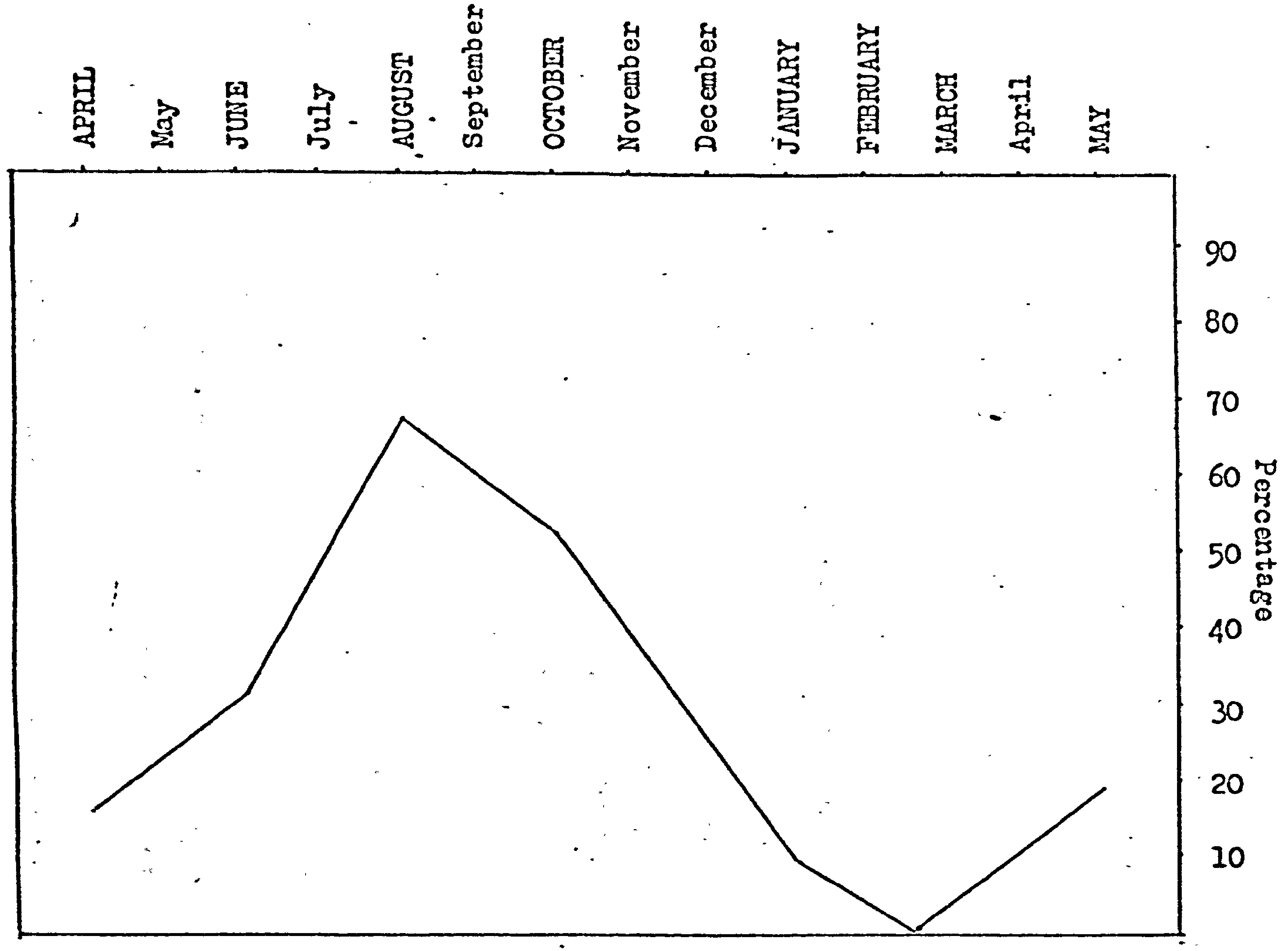
Birth seasons and peaks have been clearly demonstrated in many primate species, including free-living Japanese macaques, Macaca fuscata, and the captive colony of Macaca mulatta living in semi-natural conditions on Cayo Santiago. Evidence of birth peaks is also available for this latter species in the wild (Lancaster and Lee, 1965). The only evidence on birth periodicity in C.aethiops is that given by Starck and Frick (1958) for C.a.aethiops in Ethiopia. Their conclusions were based on uterine examination of shot material. On this basis they conclude that the species has a birth season that is synchronised to coincide with the onset of the long rains.

On Lolui there was a marked birth season. The typical pattern of births within a single group can be seen in Table 10. The pattern for a large sample of the population is shown in Fig. 10. This graph illustrates the number of adult females carrying infant ones expressed as a percentage of the total number of females counted. The method of estimating was to spend one day of each study period in a survey of as much of the island as possible, counting just adult females and infant ones. The total number of females counted on these occasions is thus often high, and the size of the sample is such that it may be considered a reliable estimate of trends in the whole population. The total numbers of females for the relevant months were; April 1963, 624; June 1963, 419; August 1963, 273; October 1963, 294; January 1964, 224; February-March 1964, 247; May 1964, 224.

As was pointed out in the section on techniques and definitions, infant ones are only classed as such for the first five months of life.

Fig. 10

Number of adult females carrying Infant ones as a percentage of total females observed.



Months typed in capital letters are those in which observations were made.

Thus the absence of infant ones in February-March 1964 indicates the end of the birth season between the previous September and October. The evidence from individual group studies upholds this. Field evidence indicated the onset of the birth season about half way through April and lasting for six months until mid-September. No births were observed in the north-west peninsula after October 1963 until the first birth of 1964 which occurred about 2nd May: the infant belonging to Group 20 and being about a week old when first observed. Many adult and subadult females were clearly pregnant in this study period. JF1, a subadult of Group 1 was the first of that group to have an infant in 1964. This occurred on the night of 17th May.

There is very little information in the literature on the length of gestation in this species, and it is almost impossible to obtain reliable information from behavioural observation. The absence of sexual skin in this species also means that external signs of the state of the reproductive and menstrual cycles are not apparent. Even menstruation is sometimes only detectable by means of vaginal lavage. Copulation occurs when females are pregnant, further obscuring the picture. In the laboratory, copulation was observed up to three weeks before the birth of an infant.

Asdell (1946) says that the period of gestation is approximately seven months in C.a.sabaeus. Kenneth (1947) gives a gestation period of 213 days for the guenons. This is comparatively long compared with data for other Cercopithecidae. Hartmann (1932) gives the mean duration of thirty pregnancies of M.mulatta as 163.9, with a range of 146 to 180. The mean of 26 of these gestations resulting in viable offspring was 165.2, with a range from 149 to 180. Van Wagenen (1945) records a mean of about 168 days for M.mulatta. Spiegel (1930) gives a mean of 167 and a range of 153 to 179 for M.irus, Zuckerman (1937) gives the gestation period of a single specimen of M.radiata as 171 days, and Cole (1963) gives a range of 171 to 210 days for Macaca nemestrina. For the hamadryas baboon, Papio hamadryas Zuckerman and Parkes (1932) give a mean of 172.2 and a range from 154 to 183. And for Papio porcarius Gilbert and Gilman (1951) give a mean of 187 and a range from 173 to 193. A single Erythrocebus patas in the Bristol laboratory apparently had a gestation period of 170 days (Goswell and Gartlan, 1965). The mean figures for the four genera, based on the above information, are Macaca 172.2 days, Papio 197.6 days, Erythrocebus 170 days and Cercopithecus, 211.5 days. This is curiously long for a species which is physically smaller than the others.

Data on copulation is less easy to obtain than is that on births, as animals are easily disturbed in this activity by the presence of human observers. The extent of the inhibition, and the comparative rareness of copulation in Cercopithecus may be judged from the fact that Haddow (1952) never observed copulation in Cercopithecus ascanius and concluded that it must be a nocturnal activity. It is unlikely that copulation took place after dark on Lolui, as animals were only rarely heard or seen moving after taking up their sleeping positions.

Sade and Hildreth (1965) noted a seasonal cycle in testis size of C.a.sabaeus on St. Kitts, West Indies. Detailed histological analyses of the material collected are still in progress, but the preliminary data may be taken as indicative that this exotic population almost certainly has a copulation season. Detailed data obtained from Group 1 on Lolui Island, which was that least likely to be inhibited by the presence of the human observer support the finding of Sade and Hildreth, although no seasonal variation in testis size was apparent from field observation only. The data are illustrated in Fig. 11. Copulation is here defined as copulation to the ejaculatory pause, when the mounted male, having finished thrusting, and presumably having ejaculated, leaves the penis in the vagina of the female for up to five seconds before withdrawing it. Displacement and incomplete mounts were therefore excluded, as were those observed during play of infants. It can be seen from Fig. 11 that only one copulation was observed in Group 1 during August, whereas in October over 30% of the total copulation observed in the group took place. It continued at a relatively high level until March, declining with the onset of the birth season. The relationship between the birth and copulation seasons is shown in Fig. 12. When the majority of adult females are carrying infant ones, very little copulation took place.

As the onset of the birth season occurs in mid-April and the

Fig. 11

Total number of copulations in Group 1 between June 1963 and May 1964.

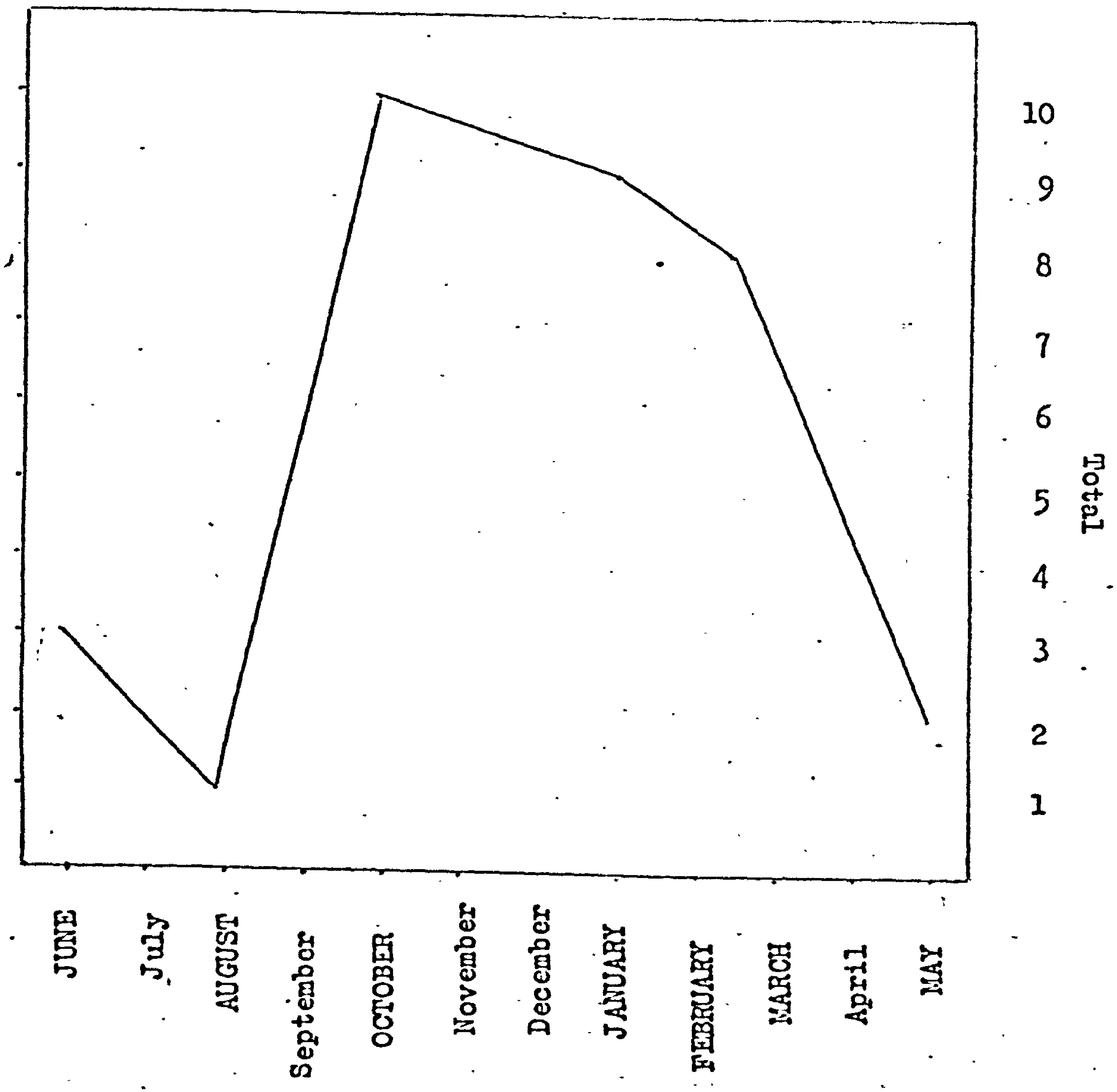
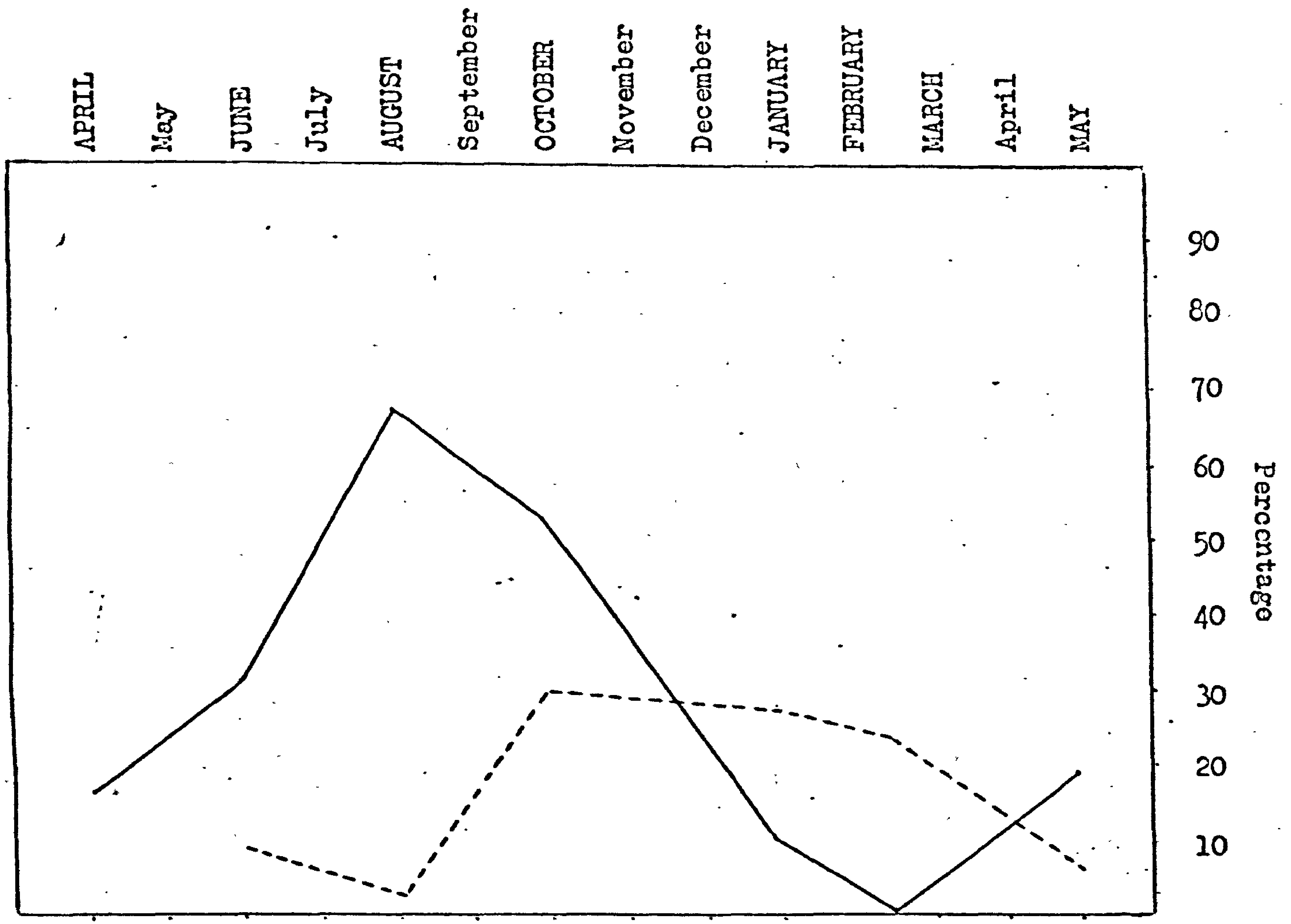


Fig. 12

Percentage of adult females with Infant ones in population sample and percentage copulations in Group 1.



Solid line = births, dotted line = copulations.

onset of the copulation season at the beginning of October, it is possible to make at least an approximate estimate of the length of gestation in this population, although it cannot be other than an extremely rough guide. The period between the onset of copulation and the onset of births is approximately 197 days, and that between the peaks of copulation and the maximum number of infants is also approximately the same. It can be seen that this estimate is higher than the figures obtained for *Macaca* and *Erythrocebus* and very similar to that of *Papio*, and lower than previous figures given for *Cercopithecus*.

The beginning of the birth season corresponds to the middle of the period of heavier rain. The rainfall increases significantly in March and remains fairly heavy during April and May, whereas the birth season begins in mid-April and lasts until mid-September. The onset of the period of heavier rains coincides with a dietary change when very little food is eaten that is neither foliage nor fruit. This coincides with a significant change in the distribution of groups in the territories; a marked tendency being observed for the group to become a closer unit at this time. It is possible that all these factors are associated with the adaptive significance of a discrete and synchronised birth season.

DAILY ACTIVITY PATTERNS AND INDIVIDUAL BEHAVIOUR

HOME RANGES AND DAY RANGING

Home range as defined by Burt (1943) is that area normally covered by an individual in its day to day maintenance and social activities. It is distinct from territory which is defined as a defended area of the home range. The *C.aethiops* population of Lolui is strongly territorial and the group boundaries are well defined and defended by several behaviour patterns. The home range of a given group therefore only rarely extends beyond the territorial boundaries, and then only for short periods. In over 500 observation hours on Group 1, less than two hours were spent in other territories. Part of this time was spent in an area over which the only change in "territorial ownership" was observed. These details are discussed more fully in the section on territorial behaviour.

The size of territories on Lolui is extremely small (Fig. 13). The mean area, based on an estimated population size of 225 individuals per square mile and a mean group size of 12.3 individuals, is .06 square mile per group. This estimate includes the grassland area and it is likely that the actual area per group is somewhat smaller. The area occupied by Group 1 is .03 square mile, and that of Group 4 .034 square mile.

Carpenter (1940) gives what is apparently the smallest previously recorded home range area for any primate species for three groups of *Hylobates lar* in north-west Siam. These were .046 - .078 square mile, .093 - .117 square mile and .093 - .156 square mile. The group sizes of this sample ranged from 3 to 6 animals.

Jay (1965) gives an estimate of Presbytis entellus home ranges of between one half and five square miles, with a group size range from 5 to 120.

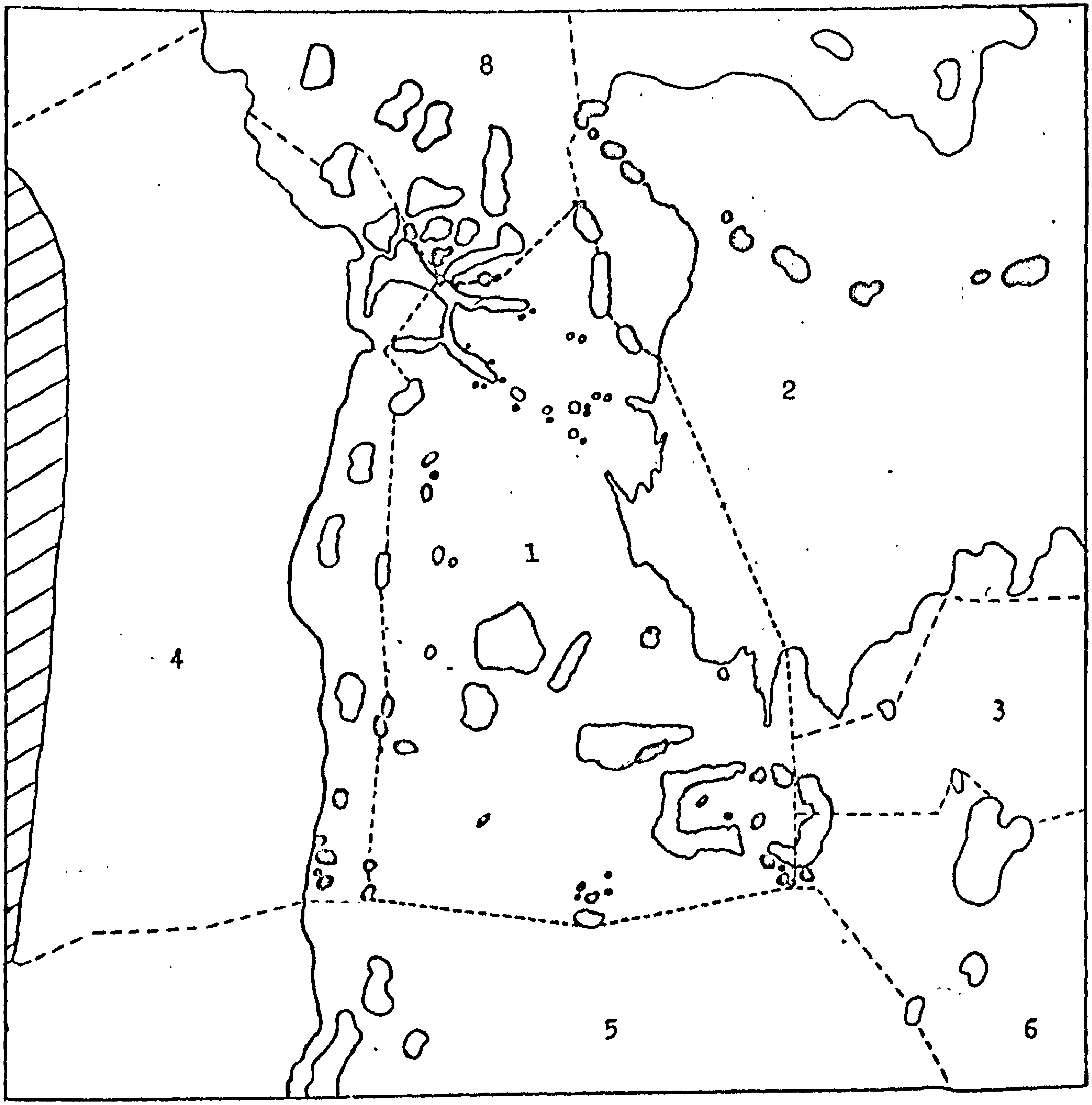
Fig. 13 covers an area of approximately .16 square mile, and the territories of seven groups impinge in this area, although only two are included completely.

It can be seen from an examination of Figs. 14 to 19 that at most seasons of the year much of the territory is covered in a single day's ranging, and most is certainly covered within a week at all seasons of the year. This complete utilisation of the territory throughout the year is in marked contrast to the position in many other primates, and indeed many other mammals, which utilise different areas according to season, a characteristic expressed in the primate literature as a "core area", see Schaller (1965) and Jay (1965). The small size of the territories and the high population density are probably the functional causes of this observed difference. The adaptive significance of the behaviour is clear, in that the closeness of the territories and their complete utilisation ensure an efficient dispersal of the population through the environment. It is also possible that the frequent patrolling of territories, which is the effective result of complete utilisation of territory by a group, maintains the integrity of the territory from invasion by other groups.

Most of the data on day ranging on Lolui were obtained from groups in the north-west peninsula, although other areas were studied in April 1963. These data were recorded in Hall and

Fig. 13

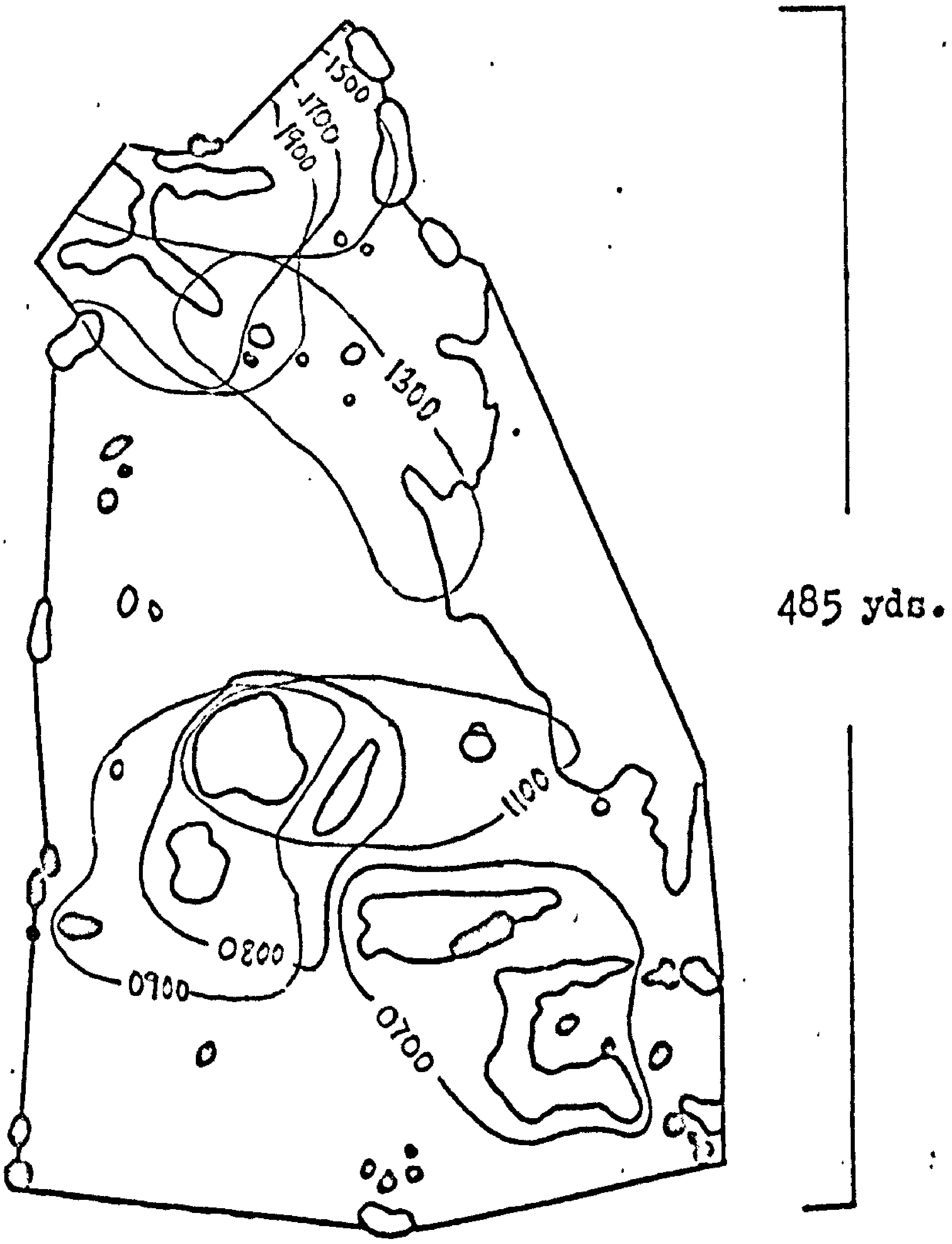
The territories of seven groups of C.aethiops on the north-west peninsula of Lolui Island.



Scale as Fig. 14.

Fig 14.

Day ranging pattern of Group 1, 13th June 1963.



Contours surround 75% of group at given times.

Fig. 15

Day ranging pattern of Group 1, 7th August 1963.

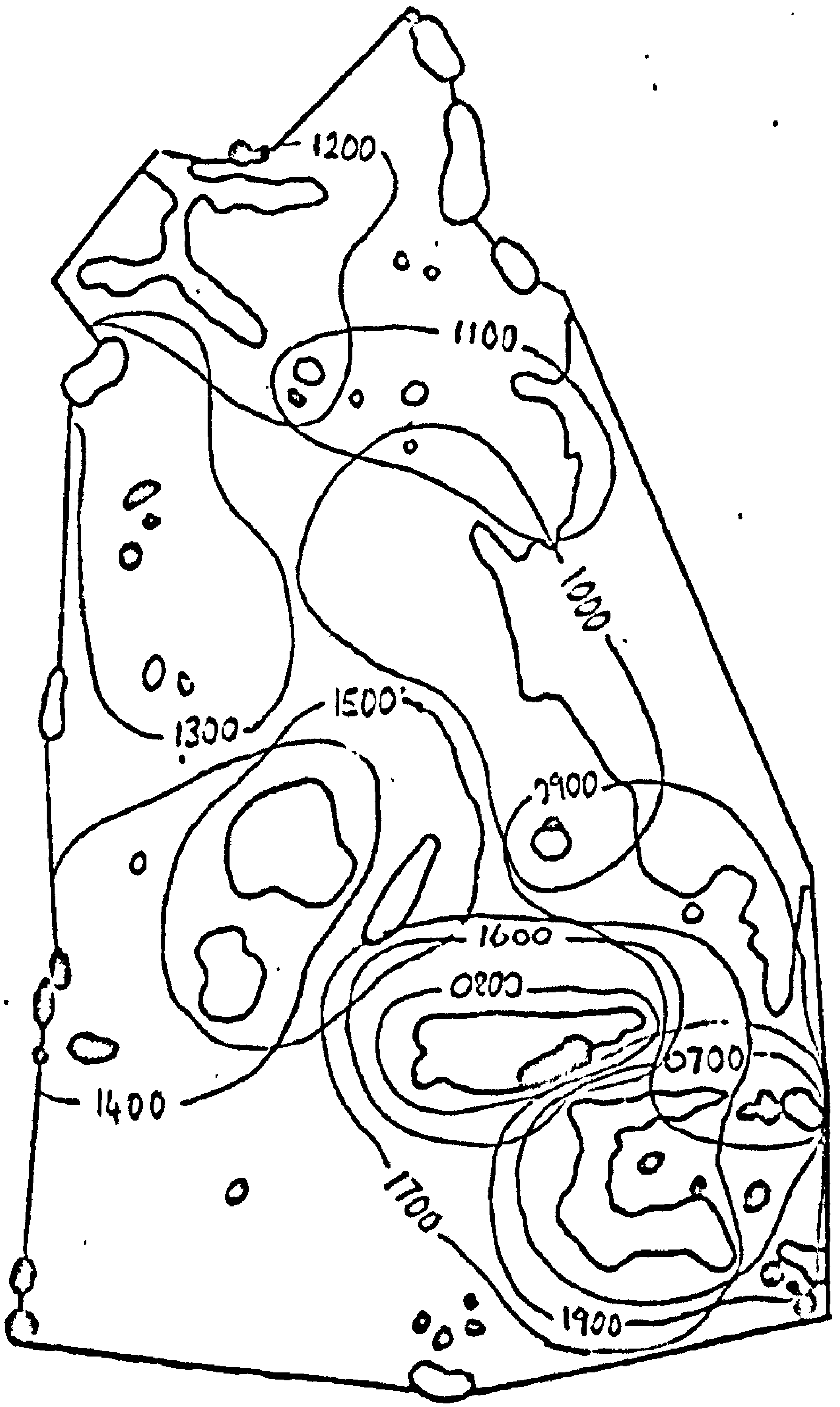


Fig. 16

Day ranging pattern of Group 1. 9th October 1963.

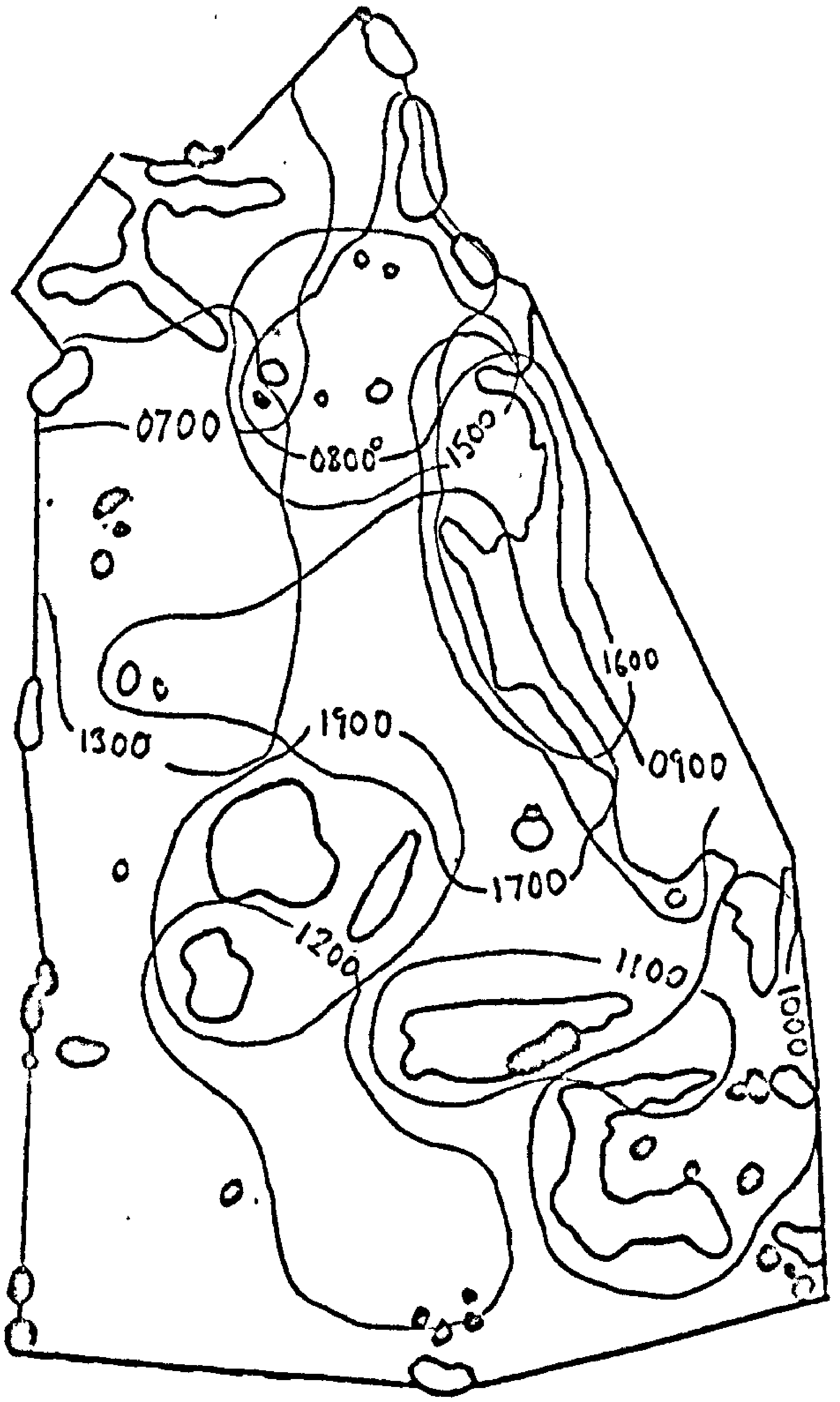


Fig. 17

Day ranging pattern of Group 1, 8th January 1964.

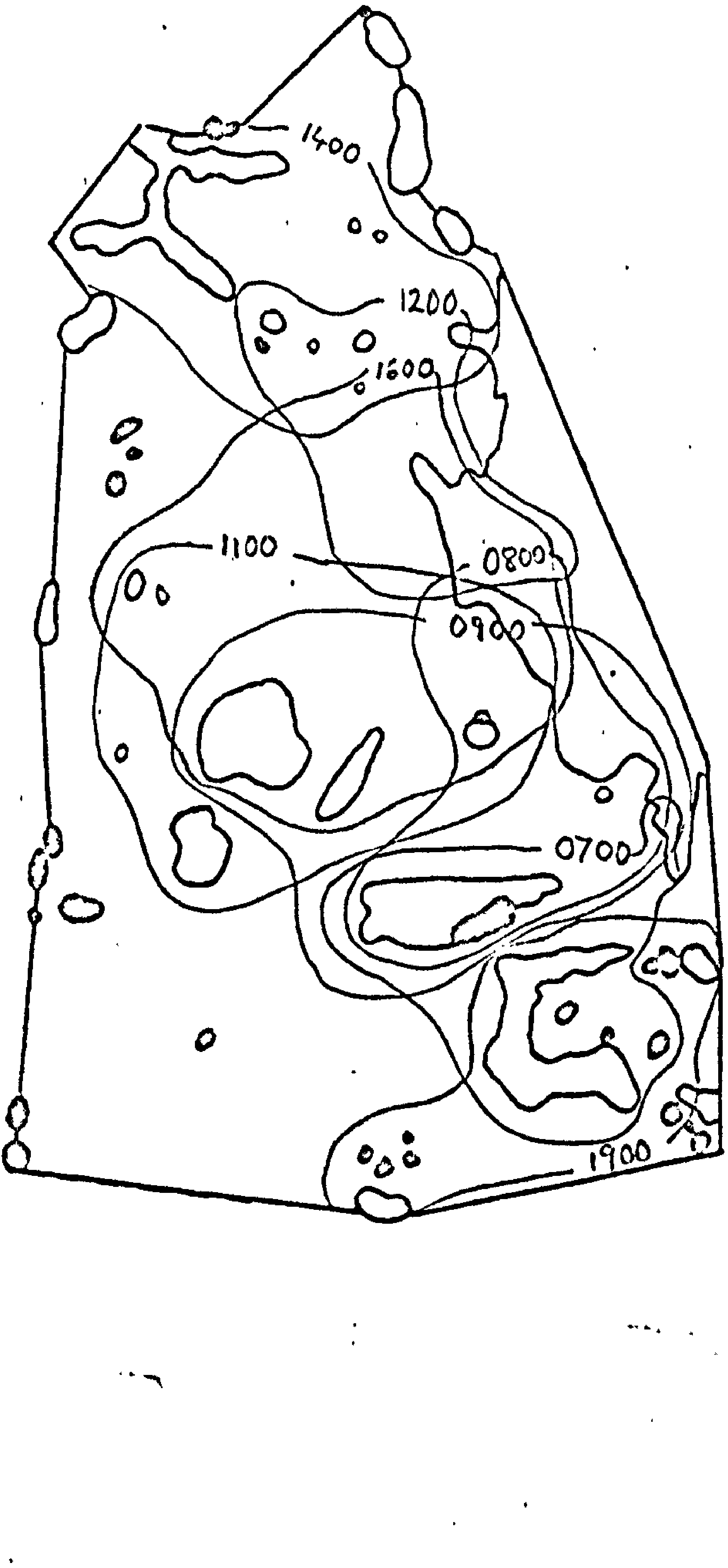


Fig. 18

Day ranging pattern of Group 1, 3rd March 1964.

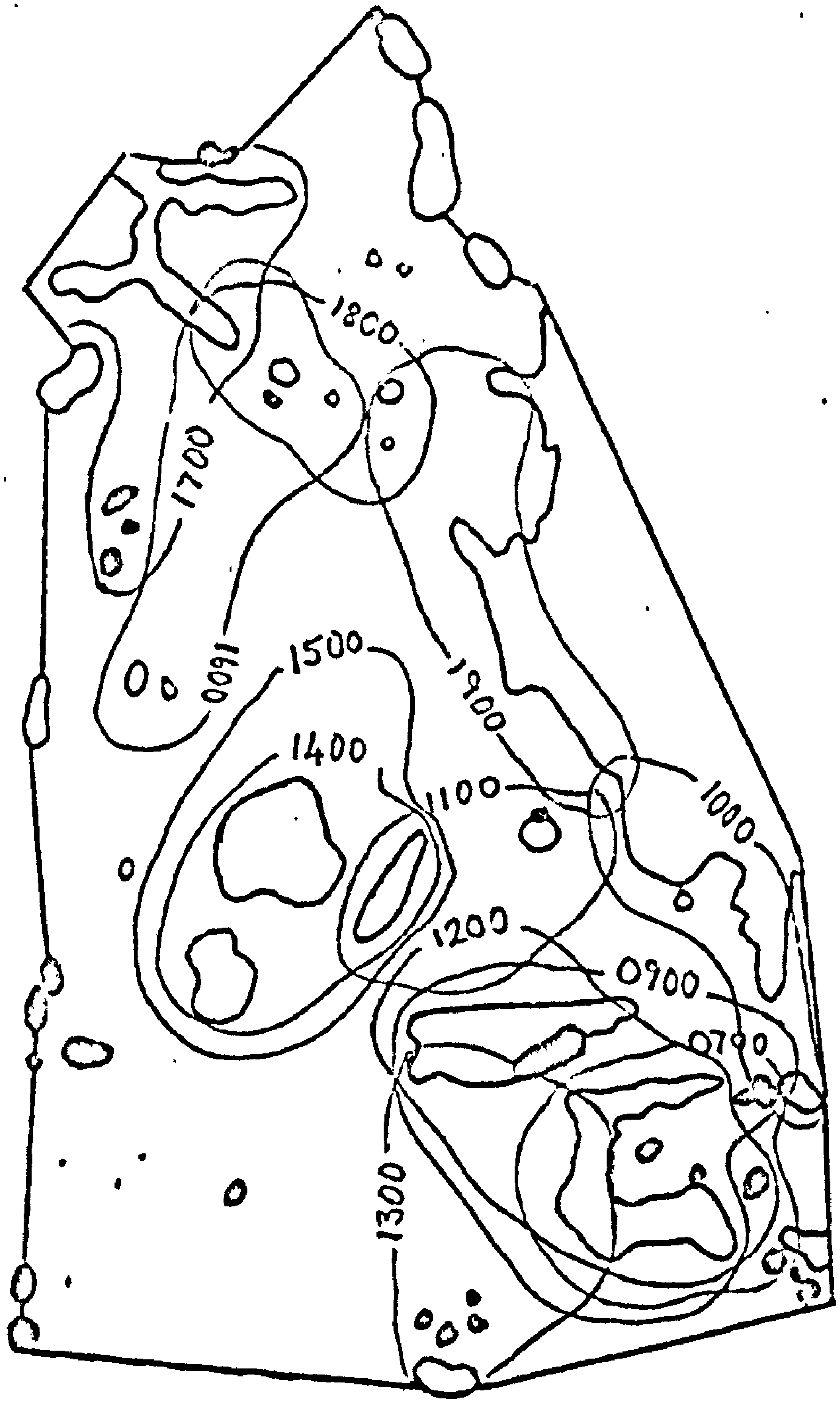


Fig. 19

Day ranging pattern of Group 1, 15th May 1964.

Gartlan (1965). Two main methods were used in plotting day ranges. The first, and that which gave most satisfactory results, was to observe a single group throughout the day, and at given periods to plot on a sketch map the area occupied by at least three quarters of the group. This method gives the type of result indicated in Figs. 14 - 19. A second method was to keep several groups under observation moving from one to the other recording the data in a similar manner. The main drawback to this method was that occasionally movements were missed. The second method was only used during the initial survey.

SEASONALITY OF FOOD SUPPLY

Lolui Island is only some six miles south of the equator, but in view of the distinct season of heavier rain, it is not surprising that there are seasonal variations in the available food supply. Certain food plants, for example Saba florida have a clear, synchronised fruiting season although in the case of Saba this is for a fairly long period (Table14). Others, such as Garcinia huillensis have a similar synchronised fruiting season, but which is rather short. Still other species, such as Canarium schweinfurthii do have a distinct cycle, but which does not appear to be synchronised, so that a Canarium in one territory may be fruiting, when an adjacent one is in a quiescent stage having shed its leaves.

Many foods have a fairly short season of palatability. This is

TABLE 14

Seasonality and relative abundance of dietary components, Lolui Island.

	April	June	August	October	January	Feb.–March	May
Saba florida							
fruit	————	- - - -	······	······		-·-·-	- - - -
leaves	- - - -	-·-·-		————	- - - -		
flowers				······		······	······
Vitex fischeri							
fruit							-·-·-
leaves	······	······	- - - -	- - - -	————		- - - -
flowers						- - - -	
Harungana madagascariensis							
fruit		-·-·-	-·-·-		-·-·-	-·-·-	-·-·-
leaves	······			- - - -		-·-·-	-·————
Garcinia huillensis							
fruit	- - - -				- - - -		
leaves	-·-·-			······		······	
Popowia buchananii							
fruit			- - - -				·····
leaves	······	-·-·-		————		- - - -	
leaf stems				······			
flowers					······		
Canthium vulgare							
leaves	······						
Canarium schweinfurthii							
fruit			-·-·-	······		-·-·-	·····
leaves	······	-·-·-				-·-·-	

TABLE 14. (continued)

	April	June	August	October	January	Feb. - March	May
Ficus capensis							
fruit							
leaves	......						
Maesopsis eminii							
fruit							
leaves	......						
Loudetia kagerensis							
leaf-stem	......	—.—.—	—.—.—			—.—.—	—.—.—
Andropogon dummeri							
leaft-stem	......	———	———	—.—.—		—.—.—	—.—.—
Insecta, Arachnida and pupae.	......	......	—.—.—	— — —	—.—.—		......
Ficus natalensis							
fruit		— — —	......		......	......	......
leaves							
Alchornea cordifolia							
fruit						......	......
leaves							
Uvaria virens							
fruit				—.—.—			
leaves			......				
Rauvolfia vomitoria							
fruit							

TABLE 14. (continued)

	April	June	August	October	January	Feb.- March	May
Ipomoaea cairica							
leaves					......		
Parkia sp.							
leaves					----		
Tricalysia niamniamensis							
leaves						......	......
"Puffball"						.....	
"Roast" insects and burnt grass.			-.-.-				

1% - 5% = ...

6% - 10% = -.-.-

11% - 20% = ----

Over 20% = ———

The data above is based on feeding hours. One feeding hour is one hour spent feeding on a given food by one monkey. One feeding hour is the minimum required for inclusion in this table, and percentages are calculated on foods reaching this criterion. Other foods are listed. The feeding hours for the months listed were, April, 98; June, 124; August, 129; October, 102; January, 130; February-March, 103; and May, 112. All data is from Group 1, except for April, which is from Group 25.

especially true of young grass shoots, and of Saba florida leaves, which are only a popular food when young and pinkish rather than green.

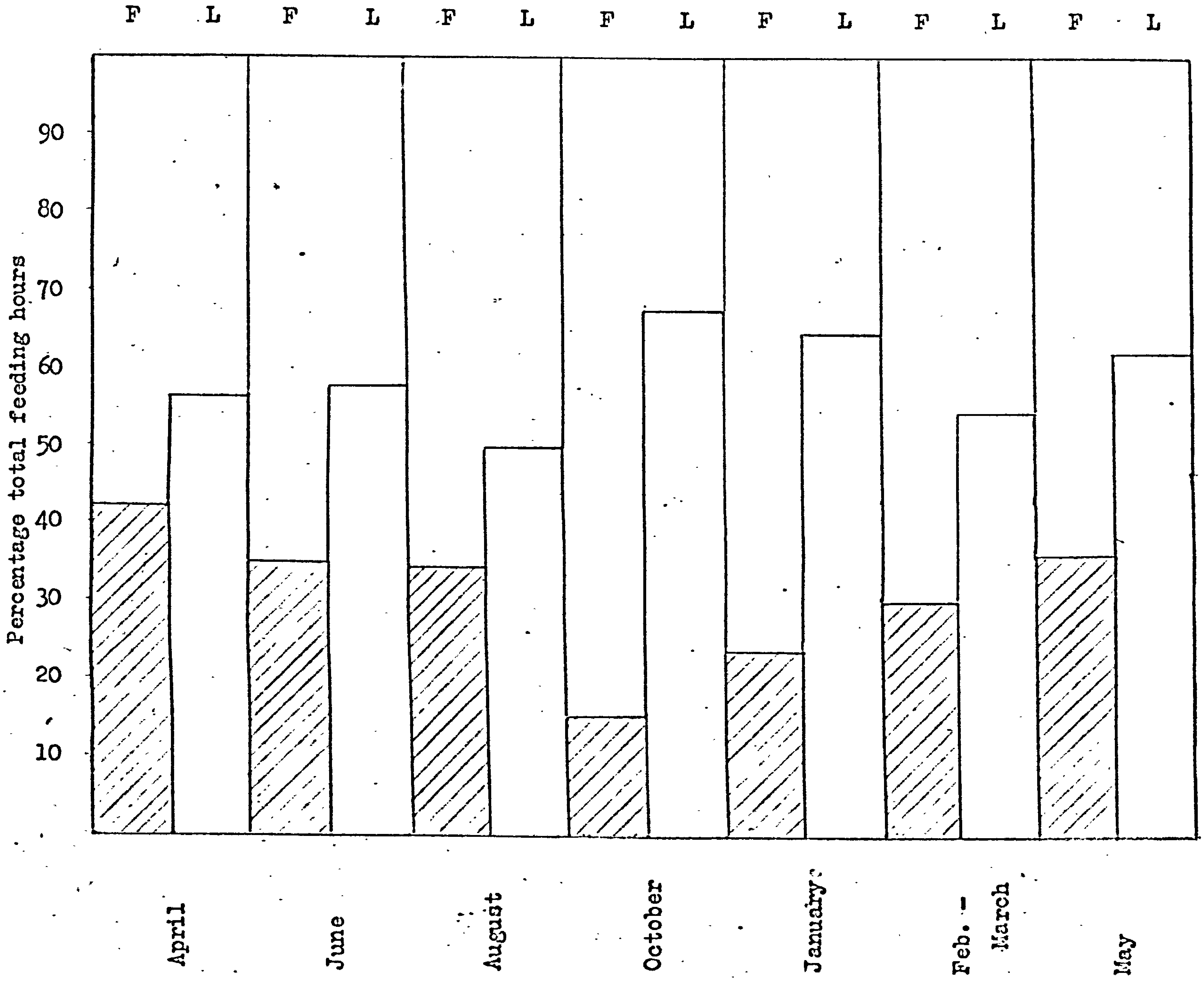
Other foods depend less directly on climatic factors. Insects which are burnt and roasted by grass fires are an extremely popular food, as to a lesser extent is the burnt grass itself, but the supply of this food is naturally dependent on the presence of grass fires and is therefore not reliable, and is practically restricted to the drier seasons.

It is important to note, however, that there is generally some fruit available throughout the year. This is perhaps not surprising since the clump and regeneration forest is almost all monkey-dispersed, and consists of species with edible fruits. There would have been intense selection by the monkey population for those species producing fruit throughout the year.

There are, however, some times of the year when fruit is in relatively short supply. Fig. 20 indicates that this is likely to occur between October and January, towards the end of the drier season. At this time a relatively higher proportion of leaves is eaten. It is also at this time that the highest proportion of food that is neither fruit nor leaves is eaten, 15% in August, 17% in October, 12% in January compared with less than 1% in April, 2% in May and 7% in June. It is also significant that at this time groups tend to be more dispersed in their territories than at other times of the year (Figs. 16, 17). The season when most young infants are being born, April to July, is a time of

Fig. 20

Relative proportions of fruit and leaves in the diet of C.aethiops, Lolui Island, throughout the year.



relatively abundant food. Few items are eaten that are not either fruit or leaves, and at this time groups tend to be less dispersed in the territories. In areas of high predation this would probably be of great adaptive significance at this stage in the life of the infants.

Another significant factor in the day ranging patterns of the Lolui population is the fact that the actual number of food species is very small. This is a direct result of the reforestation process and contrasts strongly with the position in other areas. R.C. Wingfield (pers. comm.) records that in the Zambesi valley vervets eat, "probably habitually", in the region of 250 plant species (about 300 plant foods) and 70 animal species. The hypothesis is based on an observed food list of 136 plant species eaten by the Zambesi population.

It is probable that Table 14 includes well over 90% of the plant species eaten habitually by the Lolui population. This includes only 18 plant species and about 33 plant foods, 1 fungus species and an undetermined number of insect and arachnid species. In addition to this list, a table of animal-dispersed foods of thicket and forest (Table 13) probably exhausts the number of plant species eaten by the monkey population of Lolui. This list includes 39 species which presumably constitute occasional and rare items of diet. Only three of the tree species, for example, were represented in Group 1's territory, and only by one or two specimens.

The situation on Lolui therefore means that animals do not

TABLE 13

Animal-dispersed plants of thicket and regenerated forest.

Achyranthes aspera
Ageratum conyzoides
Albizia zygia
Aloe sp.
Arthropteris orientalis
Asripomoea grantii
Asystasia gangetica
Bridelia micrantha
Celosia trigyna
Coleus latifolius
Cyanotis lanata
Cyathula prostrata
Erlangea cordifolia
Eugenia bukobensis
Ficus sp.
Fimbristylis hispidula
Hibiscus calyphllus
H. surrattensis
Justicia flava
Lindernia sp.
Mikania cordata
Morinda lucida
Oldenlandia affinis
Pachystela brevipes
Pellaea quadripinnata
Phaulopsis sp.
Polygala luteo-viridis
Pteridium aquilinum
Pupalia lappacea
Sansevieria sp.
Sapium ellipticum
Secamone africanum
Sida cordifolia
S. rhombifolia
Thunbergia alata
Tinospora caffra
Trichilia sp.
Triumfetta rhomboidea
Urena lobata

have to move large distances during the drier seasons in search of food. C.K. Brain, for example, (Gartlan and Brain, in press) records a group of C.aethiops moving a distance of 11 miles in less than 24 hours, in the Wanki National Park, Southern Rhodesia. Indeed, such behaviour would be impossible in view of the strongly territorial nature of the population. It also means that the number of discriminations that have to be learnt in order to feed is remarkably small. During the second study period approximately 300 bananas, which do not occur on Lolui, but which are known to be a favourite food of mainland groups, were distributed throughout the north-western peninsula on rocks, termite mounds and in clumps. Not one of these was eaten nor was the skin removed. And observation of Groups 1 and 2 during this period only showed occasional olfactory investigation, and only once was an animal, an adult male, observed to pick up a banana. The animal sniffed the fruit, dropped it and moved away.

The seasonal fluctuations in food supply are variations in the distribution and palatability of food rather than, as occurs in other areas, its presence or absence. As these variations in supply are in some cases seasonal, and in other cases cyclical but not seasonal, and in other cases dependent largely on fortuitous factors, it is not to be expected that there will be any strong correlation between the seasons and such parameters as the total distance travelled in a day.

In estimating the distance travelled per day and the dispersion of groups, the method shown in Figs. 14 to 19 was used. At intervals of one hour the position of at least three quarters of the group was noted and plotted on a sketch map giving a "contour ring". Day range distances were then calculated by determining the distances between the centre of successive contour rings. This measure is to some extent an abstraction since it does for the most part not take account of extreme movements, which often were not included within the contour, nor of individual movements between the times that samples were taken. Nevertheless, it provides a statistical measure useful for comparing distances moved at different seasons.

Group dispersal was measured by taking the mean of the longest and shortest diameters of the contour ring. This gave a dispersal index in yards that could be used to indicate the relative differences in dispersal throughout the year.

The distances travelled at different times of the year, the dispersal data and the time spent in grass ranging are indicated in Table 15.

The relations within these categories, the extent and significance of seasonal variations of each pattern were analysed by means of a Mann-Whitney U test. A one-tailed test was employed as directionality was predicted, and the required level of significance for rejection of the null hypothesis was .05%. For these calculations February, March, May and June were considered as the season of heavier rain, and January, August and October were considered as the "dry season" although in fact some rain fell at all months of

TABLE 15

Mean time spent grass ranging, day range distances and dispersal of Group 1 throughout the year.

Date	Time in in grass	Day range distance	Dispersion index
June '63	2.06	657	95
August '63	3.22	1146	117
October '63	3.58	1254	119
January '64	2.42	863	162
Feb-March '64	3.92	978	108
May '64	3.07	513	107

the year. The reason for the inclusion of June in the season of heavier rain, when in fact it has very little, is justified by the fact that the ecological effects of the heavier rain are still very pronounced at this time; the numbers of young green leaves, grass shoots etc., are particularly high, and in the proportion of leaves to fruit in the diet, June is more comparable to the "rainy season" than to the "dry". (Fig. 20.)

A Mann Whitney U test comparing the time spent in grass ranging in the "wet" season and the "dry" season gave a probability of .50, which for a one-tailed test was not significant. It must be concluded therefore that the duration of grass ranging is not affected by seasonal factors.

A similar calculation was carried out for the distance travelled on the day range throughout the year, this gave a probability of .1, which was also not significant under a one-tailed test and it must therefore be concluded that the distance travelled in a day is also not significantly affected by seasonal fluctuations.

A Mann Whitney U test on the "dry" and "wet" season data on dispersal of the group indicated that this probably was affected by seasonal factors. The exact probability was .05. There are probably several related factors explaining this phenomenon. The difference in the nature and disperson of the food supply at the onset of the period of heavier rain has already been described. But about one month after these ecological factors have caused a difference in the patterns of dispersion, the birth season begins, and the effect of infants is to increase group cohesion; an adult female with a newborn infant tends to seek the company of other animals rather than to remain isolated. Thus the dispersal pattern dependent on ecological factors is reinforced by social factors.

In view of the observation that distance travelled in the day range did not show systematic seasonal variations, and that dispersal patterns were affected, it was not surprising that these two behaviour patterns did not show any strong correlation. A Spearman rank order correlation coefficient gave a value of $r_s = .6$, which for an N of 6 was not significant. Likewise, no correlation was observed between the distance moved per day and the duration of grass ranging ($r_s = .66$) nor between dispersal and the duration of grass ranging ($r_s = .22$), which is not surprising in view of the fact that dispersal shows seasonal fluctuations whereas grass ranging does not.

PROXIMAL CLIMATIC FACTORS AND DAY RANGE

Seasonal climatic variations appear to affect group dispersal indirectly through their influences on food availability and dispersion. Proximal climatic factors, on the other hand, appear to affect the temporal aspects of day ranging. The two most important of these proximal factors are rain and heat. It has been demonstrated that the duration of grass ranging throughout the year is not subject to seasonal fluctuations, however the timing of expeditions is affected. In the season of heavier rain, grass ranging does not generally take place until the grass is dry (Fig. 22) and is therefore delayed after rain or an exceptionally heavy dew. Similarly during this same period the onset of feeding may be delayed, but apparently the total distance moved by the group is not affected (Fig. 21). Fig. 22 also indicates that grass ranging does not occur during the hottest part of the day, especially in the "dry" season. A clear pattern of early morning and late afternoon grass ranging is indicated. During the middle of the day feeding tends to take place on the inside of vegetation clumps, where animals are shaded from the heat of the sun.

Fig. 21 indicates the time at which feeding started in group 1 throughout the year (The onset of feeding is here defined as five or more animals of the group starting to feed). It is apparent that during the season of heavier rain the onset of feeding tends to be delayed. However, that this is a reaction to proximal climatic factors rather than a seasonal variation is demonstrated by the fact that throughout the rest of the year, a sudden heavy shower or a heavy dew (indicated in Figs. 21 and 22 by an asterisk) has a similar delaying influence.

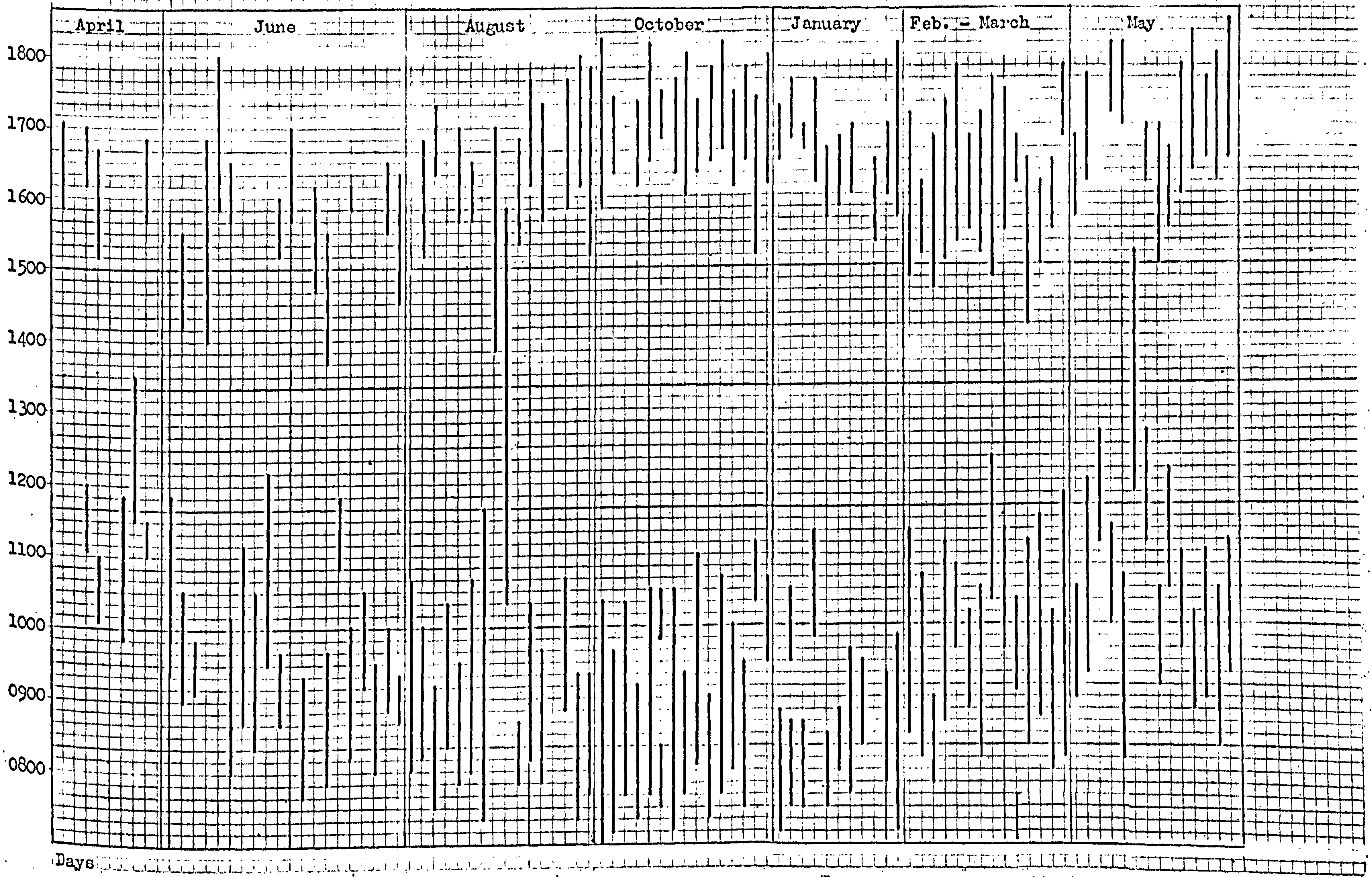
Fig. 22 indicates the onset and duration of grass ranging. This behaviour pattern is here considered as distinct from the mere crossing in grass between vegetation thickets. In general, if an animal or a group of animals left a thicket and crossed in grassland to enter another thicket almost straight away, this is not considered as grass ranging.

Fig. 21

Beginning of feeding activity of Group 1 during periods indicated.

Fig. 22

Onset and duration of grassland ranging of Group 1 during periods indicated.



It is clear that rain or heavy dew also affects grass ranging in that the onset is delayed. But the picture here is somewhat complicated by the fact that this behaviour pattern is easily inhibited by the presence of human observers. Even after groups have apparently habituated to the presence of a human observer and show neither alarm nor threat behaviour at his presence, the amount of time spent in grass ranging is reduced. This is illustrated by the data on the mean number of hours per day spent in grass ranging. In April 1963 Group 1 spent a mean number of 1.19 hours per day in grass ranging, whereas in February-March 1964 the figure was 3.92 and in May 1954, 3.07 hours. There was no apparent difference in seasonal factors nor in proximal climatic factors to account for the observed difference, which must therefore be attributed solely to the presence of a relatively unknown human observer.

This observation is matched by the fact that animals discovered in grassland never threaten or give more than single alarm calls whilst in the grass, but run to the nearest vegetation cover and threaten and call from there.

Other climatic factors such as wind apparently had little effect on the normal behaviour patterns of the population. The inhibiting effect of rain on the starting of the day's activities has been mentioned, but frequently rainstorms occurred when the animals had actually begun their day range. If the rain was not heavy, no effect was noted, except that animals were never observed in the grass when rain occurred, largely because rain during the day occurred most frequently during the season of heavier rains, when the grass tended to be wet from the overnight rain delaying the onset of grass ranging. However, if the rain became heavy whilst animals were feeding in the thickets, feeding would cease. There was no evidence that animals actually sought shelter, and animals which were on the outside of the canopy at the beginning of a heavy shower tended to stay there. However, the sleeping posture was generally adopted in these circumstances, animals sitting in the normal sitting position with the head bent low over the chest. (see section on postures). This observation is similar to that of Goodall (1963) on the chimpanzees of the Gombe Stream Reserve.

FEEDING PATTERNS.

There was no evidence on Lolui of a "burst" of feeding in the early morning such as that recorded by Haddow (1952) for Cercopithecus ascanius. The only apparent differentiation of this period lay in the fact that there was less selectiveness at this time. Thus Garcinia huillensis fruits, which apparently are only fully acceptable as food when fully ripe, would be eaten with a rejection rate of about one in ten during the first hour's feeding, but after the second hour the rate would rise to about one in four during the third hour. This fruit, which is about the size and shape of a plum, was a good indicator of food selectivity as the rejection was very clear. In all cases the fruit was picked by hand, a small piece of skin was removed with the incisors, and the pulp sniffed, rejection consisted then of merely dropping the fruit.

An examination of the rejected fruit showed that over 90% were affected by a parasitic gall fly. There was, however, no discernible difference in taste between the rejected fruit and normal healthy fruit as far as the observer could tell.

C.aethiops has capacious cheek pouches, and the normal pattern of feeding when feeding on fruit is to fill these pouches and then sit, chew and swallow the contents. This did not seem to apply when grass or insects were being eaten. The food is moved from the pouches to the teeth for chewing by means of muscular contractions of the cheek muscles, and by tongue movements. However, in several very old individuals the pouches had apparently lost much of their elasticity and in these cases transfer from the pouches to the palate was often achieved by means of pushing with the knuckle against the outside of the pouch.

The actual capacity of the cheek pouches is considerable. When the experiment on artificial feeding was carried out on Group 2, an adult female was once observed to put almost an entire half pound of shelled peanuts into her cheek pouches. In such cases the entire shape of the face was altered from the normal ovate outline to an almost rectangular shape. (Plate 15). This extent of pouch filling was not normally seen in day to day feeding, the only exception being when puffballs were discovered, when an animal would attempt to put the entire fungus, sometimes about the size of a large orange, into the cheek pouches.

Plate 15. Members of Group 2 feeding on shelled peanuts in grass. The adult female in the centre of the group has her cheek pouches so full that the normal facial outline is considerably distorted.

The normal social patterns of behaviour, and especially the normal level of aggression in a group is drastically altered in the presence of what have been termed "preferred foods". The biological or adaptive significance of the behaviour is not immediately apparent, but it does emphasise the extent to which generalisations based on the provisioning of groups, or the determination of social structure by means of fighting over food should be approached with caution. Evidence will be presented in the section on social behaviour which indicates that in the Lolui population artificial feeding increased the rate of aggressive incidents by about seven times.

Feeding in grassland.

The total time spent in grassland ranging by Group 1 throughout the 99 days in which they were observed was 280 hours, a mean number of 2.82 hours per day. In addition to this, another two hours per day may be spent on the ground either crossing between clumps of vegetation or foraging on the ground actually inside the vegetation clumps. Thus under normal undisturbed conditions, between one third and one half of daylight hours may be spent on the ground. This gives an indication of the ease with which the population exploits both aspects of the Lolui environment, and indicates also the importance of grass ranging in the daily behaviour of the group.

The types and amount of food taken in grassland expeditions are subject to various factors. Grass of the species Loudetia kagerensis and Andropogen dummeri is eaten at most times of the year, but especially when new shoots appear during the season of heavier rain, or in grassland areas where the grass cover has been removed by grass fires. New stems are eaten entire, being picked either with the hands or with the teeth. Older shoots are treated differently; the entire flowering stem and foliage sheath is picked, by hand if this is sufficient, but is frequently bitten off at ground level if it is too tough. There is then a great deal of individual variation in whether the foliage sheath is stripped from the flower stem or not. Many animals having picked the stem merely bit off about one and a half inches of stem and sheath that was nearest the ground and dropped the rest. Many animals however strip the foliage sheath from the stem, a motion that is carried out extremely rapidly with the incisors whilst the stem is held either with one hand or two. About the same amount of the softer foliage stem is then bitten off and eaten and the rest discarded. The variations in this behaviour pattern did not appear to be systematically related to the age-sex category of the animals, nor to the state of the grass. The stripping of the sheath from the stem was usually accomplished in between one and two seconds. No "dusting" or removing of adhering soil particles was observed on Lolui, as was observed by Hall and DeVore (1965) in the baboons of South and East Africa.

After a grass fire large numbers of "roasted" insects and burnt grass stems are usually found on the ground. On Lolui these fires were most common in June and July. Such burnt areas were very popular feeding areas and as soon as the flames had passed, entire groups would come down into the area and feed from the debris. As a result of this the normal grey fawn colour of the animals would be altered to almost black.

Another principal food taken in grassland expeditions are insects and arachnids. These are taken throughout the year, but at particular seasons certain species are especially prevalent. The two main ones of importance in the diet of the monkey populations were "lake flies", small Chironomids, 1-2mm in length which swarm mainly in August. In the early morning these swarms are sometimes so thick that they have the appearance of a low cloud hanging over the island. They are too small to be of individual interest to the monkeys, but it happens that at this season spider webs are especially common on the seed heads of both Loudetia and Andropogen and often many hundred of these small flies are caught in single webs. At this time, monkeys in their grassland trips pull down the grass seed head with one hand, and remove the web full of flies either with the other hand or with the mouth, and the entire web is eaten.

Another insect which appears seasonally in swarms is a grasshopper Acrida sp. which appears in October. This species is known in Uganda as "nsenene" and is a popular native delicacy when roasted. Groups in grassland during the nsenene season spend a great deal of time chasing the insects, which are low-flying, and are caught either with one hand, or with a hand-clapping movement, the insect being trapped between the two palms. This latter movement is often performed with a leap to catch an insect which is flying too high to be caught by other means.

Not all the grassland ranging time is spent in feeding, however, and a considerable amount is spent sitting on rocks or termite mounds, resting and grooming. It could not be established, however, that relatively more time was spent in resting and grooming when in grassland than occurred in vegetation clumps. However, during the resting and sitting on rocks and termite mounds, much urination and defaecation took place, and the role of this in the reforestation process has already been discussed in the section on the ecology of the island.

Feeding in clumps and thickets.

The majority of food taken in thickets and vegetation clumps is either fruit or leaves, but this is by no means exclusively the case. Many insects and larvae are also eaten here. During the season when there is least rain very high proportion of what was probably the egg-case of an arachnid were to be found in leaves especially of *Vitex* and *Harungana*, which were curled up by the presence of the egg case. Animals often spent a considerable amount of time searching for these characteristically curled leaves (Plate 16), which were then unrolled with both hands, and the egg-case bitten off and swallowed. The number of leaves unrolled for each edible egg-case was sometimes as high as twelve. A juvenile male was once observed to spend an hour and a half of the first feeding of the day - i.e. before it had presumably eaten any other food, in searching for these egg-cases, and probably only ate no more than twenty during this time.

Caterpillars and other larvae are another frequent food in vegetation clumps and thickets, but they are not searched for systematically in the same way. These are only eaten after they have been killed, this consists of a rubbing, or dusting motion of the larva against the branch or trunk of a tree. Several rubs are usually carried out with the animal generally not looking at what it is doing, this is followed by a close inspection to see

Plate 16. Juvenile male searching in Canarium for the characteristic curled leaves containing ararchnid egg-cases.

whether it is dead; if not the process is continued, until finally the larva is put into the mouth and eaten. Arachnids are occasionally rubbed in this manner, but are generally put straight into the mouth.

Fruit Foods

1. Saba florida

In this section "fruit" is used in the vernacular sense and not specialised botanical sense. The fruit of Saba florida is about the size, shape and colour of a large Jaffa orange. The skin is up to half an inch thick, very tough, and until fully ripe is extremely rich in latex. The fruit is often difficult to detach from the tree and a large proportion of Saba fruits are eaten in situ. Saba fruit is a main diet component of the monkeys for most of the year, but does not occur in January and is relatively scarce in August and October (Table 14). The inside of the fruit consists of between twenty-five and thirty stones, about one inch in length, which are surrounded by an acid yellowish pulp. The pulp is fibrous and is attached to the stones.

The fruit is eaten through a hole which is made in the skin. This is apparently easier for adult males with their larger canines. The usual method is to hold the fruit in both hands, whether or not it is still attached to the tree, and to bring the mouth into contact with it, opened wide, the incisors and canines make contact, the jaw is then closed, and by a combination of mandibular and head movements, a circular piece of skin is removed. The pulp-covered stones are then removed by hand. If the fruit is slightly unripe and the pulp is exceptionally acid, the stones then tend to be put into the mouth, sucked for a second or two, then removed with the hand, and the process then repeated. This was known as the "popping in and out" or "lollipop" method of eating. When the flesh had been removed from the stone the latter was dropped, usually straight from the mouth into the undergrowth. Occasionally, with large fruit, after the initial hole had been made, the skin was then torn with the teeth even further, sometimes resulting in the fruit being split into two halves. It was not usual for a complete Saba fruit to be eaten by an individual animal at a single sitting.

If a Saba fruit is picked, the animal may eat it in the vegetation canopy, but it is usual for it to be taken to a rock or termite mound which apparently provides a firmer base for the manipulation of the fruit. The carrying is generally done with the teeth. The result of this is that the discarded stones are frequently left on the rocks or mounds along with the debris of the skin (Plate 17).

Plate 17. Skin, leaves and other debris of Saba fruit which has been carried from vegetation clump to rock in grassland and eaten there.

The inspection of these fruits to ascertain whether they are sufficiently ripe is apparently visual, and it is not common to see them sniffed. Occasionally juveniles and infant twos attempt to open small fruits, which are invariably green, and succeed only in becoming covered with the copious latex, and then spend some time trying to remove the sticky substance by self-grooming.

If a Saba fruit is accidentally dropped by an animal from the high canopy to the undergrowth, it is never retrived. The fact that the droppings were in fact accidental was clear from the fact that redirected threats were often observed in this context, occasionally at the observer.

2. Vitex fischeri

Vitex fischeri is very commonly found established on termite mounds and as the focus of thickets (Plate 9) which indicates the popularity of the fruit for the monkeys. It is commonest in May, but is eaten also in April. The fruit is about the size of a large grape, it is black, with a large stone and a pungent aromatic taste. (Plate 18).

The fruits are generally picked individually by hand, but the incisors may be used. They may be stored in cheek pouches. When eaten, the skin is removed very rapidly and skilfully, inside the mouth by the tongue and teeth, the tongue is then protruded with the skin of the fruit on the tip, it is deposited on the lips, which are then moved until the skin drops off. At no time are the hands or fingers used in this manipulation.

It appears that generally the stones are swallowed as well, and they appear commonly in the faeces at this time of the year.

Plate 18. Vitex fischeri. Bracket with fruits at bottom left of picture, upper brackets have been stripped.

3. Harungana madagascariensis

This tree, or shrub is a very common component of monkey-dispersed thickets. The fruit is eaten throughout the year, but is rarer in October. The fruit grows on brackets about the same size and carrying the same numbers as the British elderberry. The fruits are a dark golden yellow however. Animals feeding on these fruits generally pick the entire bracket with the hands and then strip the berries from it with the teeth.

4. Garcinia huillensis

This species has a restricted fruiting season, and is also subject to invasion by a gall-fly larva. The fruit is about the size and shape of a plum, and is an orange-yellow colour. The fruit is picked individually with the hands and a small piece of skin removed with the incisors, the pulp is then sniffed and is accepted or rejected on this basis. If the fruit is moderately ripe, it is put into the mouth and the rest of the skin removed in much the same way as with the Vitex fruits, and dropped to the ground. However, certain animals in Group 1 had a particular way of dealing with very ripe specimens, which were opened by removing a piece of thin skin to inspect the pulp, which was then squeezed into the mouth with the hand, through the hole. The remaining debris was then dropped from the hand into the undergrowth.

5. Popowia buchananii

This species also has a fairly restricted fruiting season. The fruit is a small berry about the size of a black currant. The berries are a very popular food when ripe and are stuffed into the cheek pouches. The stones are not spat out, and are commonly found in the faeces.

6. Canarium schweinfurthii.

This is a high canopy species, the fruiting season of which does not appear to be synchronised with any climatic seasonality. The fruit is about the size and shape of a date, and is green when unripe, but a deep purple when ripe. The flesh surrounding the stone of this fruit is relatively thin, and to the observer was tasteless. The fruit was held in the hands and the flesh removed with the incisors. The stone was rejected and dropped into the undergrowth, but was occasionally swallowed. The stone of the fruit was occasionally found on the ground having been cracked open, and on one occasion members of group 1 were seen in this activity, the stone was placed between the molars, but most of the attempts led to failure. Those that were cracked had the kernel removed and this was eaten.

7. Ficus natalensis

The fruit of this species, a small yellow-green berry, was a very popular food when in season. It was generally eaten when green and relatively tasteless. A specimen of the tree which grew near the camp had fruit which were allowed to ripen, and which then tasted sweet, but none were allowed to reach this state in Group 1's territory.

8. Alchornea cordifolia.

This species was very common, especially in those vegetation clumps and the fringing forest which were nearest the lakeside. The fruit is a ribbed berry about the size of a small grape, and when ripe is a translucent pink in colour. It was not a very popular food, and in spite of the large numbers, only formed a comparatively rare diet component. The taste was rather like a bitter raw potato.

9. Uvaria virens.

The fruit of this species are fairly hard and ripen in a small pod about two inches long. They are extremely acid. The pod was generally split with the teeth, and the fruits removed with the hands, and chewed.

10. Rauvolfia vomitoria

The fruit of this species was only observed being eaten by infant twos, and it is possible that the animals concerned were still in the process of learning about the diet components. The fruit was orange-red berries, about the size of a small pea, and these were the only diet components that were actually distasteful to the observer. An extremely unpleasant taste, which is difficult to describe, was followed by a slight burning sensation in the mouth.

Foliage foods.

1. Saba florida. The leaves of this species are only eaten when they are young, the greatest numbers appearing in October. At this time the leaves have a pinkish tinge which they lose on reaching maturity, becoming thicker and glossy. Selection of appropriate leaves is apparently visual. Leaves are not usually rejected once they have been picked.

2. Vitex fischeri. The leaves of this species are apparently only acceptable when young. The two terminal leaves are those most commonly eaten.

3. Harungana madagascariensis. This species is treated in exactly the same way as the previous one, the two terminal leaves being those that are most commonly eaten.

4. Garcinaia huillensis. The leaves of this species are generally only eaten when young. They are also apparently selected visually, as are most leaves. There is a clear colour distinction between the two, young leaves being a bright yellow-green, and older ones a darker glossy green.

5. Popowia buchananii. The leaves of this species are eaten occasionally, and are apparently eaten at all ages.

6. Canarium schweinfurthii. The leaves of this high canopy species are rather thick and covered with stiff, short hairs, and apparently only the younger specimens are eaten. Selection is visual.

7. Canthium vulgare. A small quantity of these leaves is eaten, mainly in April.

8. Ficus capensis. The leaves of this species are eaten in small quantities, again in April. These leaves are large, sometimes over 12" long, and often pieces of the leaf are torn off, sometimes leaving a characteristic ragged fragment.

9. Maesopsis eminii. The leaves of this species were observed being eaten in April, but the height of the trees was such that the age of the leaves that were eaten was not established.

10. Uvaria virens. The leaves of this species were eaten during a short season in August.

11. Ipomoea cairica. This species is allied to the Convolvulus, and is an annual. The foliage is only eaten apparently when there

is a shortage of other palatable leaves.

12. Parkia sp. The leaves are eaten again when other leaves are in comparatively short supply, but when there is a large proportion of young leaves and leaflets on this species.

13. Tricalysia niamniamensis. The small, lanceolate leaves of this species are eaten between February and April.

Other foods.

1. Saba florida. The flowers of this species (Plate 19) are eaten between October and May. The flowers are white and highly scented. Individual differences existed in whether the entire flower was eaten, which occurred in five of the Group 1 members, or whether merely the base of the corolla tube was bitten off and eaten, the rest of the flower being discarded. This was observed in three members of the Group 1. This food was located visually, but in one case an infant two was observed to approach a juvenile female who was feeding on these flowers, and to "mouth" her, a gesture which may be ritualised as a greeting, but which is frequently observed in feeding behaviour. The infant two, having sniffed the juvenile's mouth, moved about thirty yards to the nearest Saba bush which was in flower, without pausing to feed on the way, and apparently purposively, and began to feed from the Saba flowers. A considerable amount of "mouthing" was also obseved when animals were beginning to feed from the peanut pile.

Plate 19. A head of Saba florida flowers. These are an occasional monkey food, some individuals eating the entire flower head, others merely the base of the corolla tube, rejecting the rest.

The role of olfaction in the identifying of foods, and of the weaning of infants is probably of great significance.

2. Vitex fischeri. These small, mauve, slight scented flowers are picked and eaten mainly in February-March. The entire flower is always eaten.

3. Popowia buchananii. The white flowers of this species are eaten in January, but more interestingly, leaf petioles are a very popular item of diet in October. The leaves of this species (Plate 20) have a rather short petiole which attaches them to the twig, the leaf was picked with the hand, and the petiole bitten off with the incisors and swallowed; after an adult female had been feeding in this manner for about 25 minutes 186 leaves with their petioles removed were recovered from under the tree. The observer was unable to discover seasonal variations in taste or texture which might have made them preferable at any particular time, nor did the taste seem to be very different from the petioles of several other species.

4. Puffball. These fungi were only occasionally observed, but appeared to be most common in the season of heavier rain. The animal finding the fungus stuffed as much of it as possible into the cheek pouches, holding it in both hands and biting lumps out of it. The taste was very like that of a common British field mushroom uncooked.

Plate 20. <u>Popowia buchananii</u>. Leaves fruit and flowers of this species are eaten, but in October the leaf petioles are a very popular item of diet.

SLEEPING PATTERNS

A group invariably sleeps within its territorial boundaries; no exception to this rule was ever observed on Lolui. But within the territory the group will sleep anywhere where there is suitable cover. Thus Group 1 (Fig. 13) would sleep either in the high canopy vegetation near the boundary with Groups 4 and 8, the area of fringe forest near the boundary with Group 2, the clumps of vegetation in the centre of the territory, or finally the vegetation near the boundary with Group 6. The only tendency that could be detected in the selection of sleeping sites was for a group not to sleep in the same place as the previous night. The longest consecutive stretch that Group 1 slept in one location was three nights, and this was in the high canopy vegetation bordering Groups 4 and 8, and occurred in July, when the grass fire had made an area of preferred feeding nearby, causing the group to remain feeding in the grassland until almost dusk.

A further tendency was observed for animals to sleep in the area in which they were feeding during the last half hour of daylight. If a group was in a particular part of the territory at 1830 hours, there was a strong tendency for it to sleep in that area, and for it to be in the same general area at 0530 the next morning. No significant movement ever took place during the hours of darkness.

Generally, individuals of a group sleep fairly close together within a single vegetation clump, or the same area of fringe or relic forest. In the 99 days in which group 1 was observed for day-ranging and dispersal patterns, the group was split on 10 occasions. There was no apparent consistency in the groupings on these different occasions.

The usual site for sleeping is a branch at the junction with the main trunk (c.f. Plate 21). The common sleeping posture, back bent, head down almost on the chest, legs extended and slightly apart, hands resting on the branch at some point between the knees and the feet, is usually adopted. This posture is a modification of the common daytime resting posture as shown on Plate 21. Occasionally the legs are fully flexed with the knees almost underneath the chin, but this is rather rare. Infant ones sleep in the ventral position to their mothers, but infant twos and juveniles do not, although they often sleep quite close to the mother up to about two years of age even after another infant has been born to the mother.

There was no evidence of huddling, or of clusters of animals of more than one or two, and these almost invariably were of mothers and offspring. Brain (Gartlan & Brain, in press) states that in Rhodesia and South Africa the species often huddles together at night, especially when it is cold.

There is very little movement at night, and certainly none to uphold Haddow's (1952) contention of noctural copulation. The only movements that were ever encountered at night were the

Plate 21. Adult female (left) and juvenile female of Group 1 sitting in typical rest postures in Canarium schweinfurthii during a pause in their feeding activity.

direct result of disturbances. Genetta tigrina and Hippopotamus amphibius are both primarily nocturnal species and therefore potential sources of disturbance. The principal sources, however, appeared to be grass and bush fires which gave rise to shifting of positions and occasional alarm calls.

Animals never slept in the exposed high canopy. The position seen in Plate 21 would commonly be seen just prior to nightfall, but at dusk they would descend to the shelter of the understorey and take up their positions there for the night.

INTERACTIONS WITH OTHER SPECIES

The diagram of the habitats and food selection of the principal mammalian species of Lolui (Fig. 6) indicates that there is unlikely to be any large amount of direct competition resulting in frequent interspecific contacts. In fact such a direct interaction was only observed in the case of the rock hyrax, Procavia capensis, but was not uncommon with avian species.

Group 8 and a small numberof hyraxes, perhaps only three at a maximum, used the rock pile shown inPlate 3 for resting and sunbathing.

On 29th February 1964 at 1017 hrs, two adult females of Group 8 were observed sitting on one of these rocks, together with two juvenile males. An adult hyrax was also on the rock, about four feet from the nearest monkey; one of the adult females was grooming a juvenile male, the other female was grooming herself. The other juvenile male was merely sitting, looking out over the grassland. No attention was paid to the hyrax whilst it sat still, but after 9 minutes, it moved nearer the front of the rock, and nearer to the juvenile who was looking out. He looked round at the hyrax, scratched himself with his right hind leg, and rubbed his nose with the back of his hand. These are typical "displacement" activities occurring under mild stress. The hyrax continued moving towards the group and the juvenile gave a mild threat "chitter" and moved off the rock into the undergrowth. All the other animals stopped what they were doing and watched the hyrax but took no further action. The hyrax continued over the rock, and disappeared from view. The monkeys continued their grooming. There is no easy explanation for this behaviour. Hyraxes are not likely to be aggressive towards monkeys, who anyway have the advantage in terms of speed and teeth with which to deal with potential attacks.

Interactions with avian species were much more common. The general cause of these was the suddenness of approach, or the noise of the approach made by the birds. Kites, milvus migrans were very common on Lolui. They tended to perch on the top of the high canopy, especially Canarium schweinfurthii which is much frequented by the monkey population. A kite which was perched when monkeys entered the tree was generally safe, but if one landed on a tree near a monkey which was either feeding or resting, there was a high probability of its being chased. Of 47 observed instances of a kite being chased by monkeys, 32 were chased within one minute of landing in a Canarium tree. They were chased by both sexes and all classes excluding infants.

The grey turaco, Crinifer zonurus is a particularly noisy bird, having a very loud characteristic call, rather like a manic human laugh, this is generally made with a great deal of conspicuous movement. They are much rarer than kites and interactions with the species are not often observed. Of the six which were observed, five were of chases when the bird vocalised, the sixth involved a pair which was sitting on a branch in the high canopy, and which were being threat faced and "rushed" by a pair of juveniles. The birds had not vocalised, and were unwilling to move, although no nest was visible. Finally a juvenile made a grab at the tail feathers and both birds flew off.

Fish eages, Cuncuma vocifer are extremely common on Lolui, especially in the fringe forest, where they tend to have particular tree bases from which they fly out to fish. If they swoop low over a thicket, or over forest in which a monkey group is feeding or resting, they are occasionally threatened and evoke alarm calls. However, actual harassment of the birds was seen on nine occasions, and these incidents were only performed by adult males. Generally the eagle had caught a fish which was either too large or was otherwise unsuitable for taking back to the tree base for eating, and it had landed on another tree near a monkey. When this occurred, threat by the monkeys was invariable, and resulted in an adult male coming up and making a series of "rushes" at the bird until it flew off. On one occasion a young bird had caught an exceptionally heavy fish, so that it was unable to rise more than about three or four feet above the ground with it. Finally it landed on a termitarium in the grassland, in Group 5's territory. Two adult males and a juvenile male immediately dashed up through the grass where they were feeding, to the mound, giving guttural grunts, and made a series of rushes up the side of the mound, this continued for about 30 seconds, and culminated in the bird flying away with the fish.

No evidence was ever seen to suggest that any of these species may have predated on the monkey population, and in most cases the threat to the bird was a result of disturbing the monkey, but in this latter case and in the case of the turacos this seemed to be a systematic attack which was not initiated in the first place by "fright".

In view of the supposed "instinctive" fear of snakes in primates, (c.f. Thorpe, 1956) it was interesting that several species occurred on Lolui. The only common dangerous snakes were the Puff Adder, *Bitis arietans*, and *Naja melanoleuca* and although encountered by the observer several times, no interaction of these species with the monkey population was ever observed. However, the Monitor lizard, *Varanus nilocticus* was very common, but the only interaction with this species by the monkeys involved infant twos of Group 1, who twice in May 1964 were observed sitting in a *Vitex* sapling, about 5m from a monitor of about 3' in length, and watching it intently whilst it dug a hole in the sandy substrate. Twice interactions were observed with a small green snake, *Chlorophis (?) heterolepidotus*. The species is an extremely fast mover in grassland. On two occasions specimens were observed to move over rocks on which monkeys were sitting, in one case a single adult female, in the other two adult females involved in social grooming. In both cases the animals turned to look at the snake, but took no further action and carried on their previous activities when the snake had moved off the rock. No vocalisation or facial expression indicative of fear was observed.

These observations may perhaps be taken to indicate that learning is involved in the reaction to snakes. An experiment with a harmless garter snake in the Bristol Department on the captive group evoked reactions of extreme fear.

The actual reaction to the observers in the first survey in April 1963 was very variable, and this was later determined to depend mainly on the number of juvenile males in the group. This point will be dealt with in more detail in the appropriate section. But the reactions which were observed, the chirrups, chitters, honks and threat postures were not those which were evoked by the presence of African fishermen, which elicited very different reactions. At all times, if an African fisherman were observed approaching the group - and occasionally even at distances of as much as three quarters of a mile - the reaction of the monkey observing the intruders was to give a soft alarm call (sac), which is very difficult to hear more than 20 yards away. The reaction to this was for all monkeys in the grass to rush to the nearest vegetation cover, descend to the undergrowth and to remain quiet and immobile until the danger had passed. These two reactions were generalised, so that all Africans were treated as potential predators and all Europeans as annoying intruders.

An interesting postscript testifies to the validity of this observation and the duration of the learning. An American negro postgraduate came to Bristol in 1965. He was to be shown round the primate laboratories and was first shown the patas monkey colony, some of which had been in captivity for four years, and has as far as is known never seen a negro during that time. The reaction of the monkeys was immediate panic, on a scale similar to that induced by the garter snake. The same reaction was observed in the vervet colony, which had only been in captivity for about a year. As a control, a strange European was brought into the colony some time afterwards, and although some fear was induced, it nowhere approached the panic induced on the first occasion.

INVESTIGATIVE AND ALARM REACTIONS

Developmental information

The two incidents of infant twos sitting and watching a monitor lizard digging are typical of the "interest" or investigation showed by this age class of animals. It was especially clear with reference to the observer. If during the course of day ranging, the observer sheltered from the heat by sitting in the shade of a vegetation clump, the group as a whole took little notice, after they had become habituated. But there was one exception. In February-March and May 1964, there were, as has been noted, six infant twos in Group. 1. Throughout these months they were found during daylight in a play-group, composed only of these individuals. The entire group tended to come into the tree under which the observer was sitting, and come and look at him. The fact that they were physically capable of threat gestures was shown by the fact that any sudden movement by the observer resulted in "threat chitters" by the infants. But if there was no sudden movement, they would come closer and closer, sometimes as close as three feet, watching. A play group which has been inspecting the observer, but which was disturbed by his operating the camera is shown in Plate 22.

Plate 22. Play group of five infant twos, who have been "inspecting" the observer, and who have reacted to him moving to photograph the group by threat and displacement scratching. The animal at the top of the picture has just completed a "threat jerk",

the one at the bottom is scratching himself, the
two at centre-left are preparing to dash off.

The intense interest shown in the observer by this age class is indicated by the fact that very typically they would investigate the observer from all anges, moving the head to one side, or even turning completely upside down to look at him. This occurred normally only after a prolonged period of inspection. (Plate 23). This posture had no counterpart in the behaviour repertoire of older animals. It must be emphasised that it was not a threat posture, no vocalisation or facial evidence of this ever being indicated, and is more likely to be merely an attempt at varying the qualities of the stimulus in an attempt at a more comprehensive assessment.

The strong motivation of this investigative behaviour, and the fact that it probably precedesthreat in development, is shown by the fact that on nine occasions a juvenile was seen in association with an infant two, the former threatening and chittering at the observer. In spite of the proximity of the two animals, not more than four feet in all cases, the infant two in all cases did not threaten, but merely looked intently at the observer.

This investigative behaviour seems only to coincide with the play-group stage of development, and by the time animals have reached the juvenile stage of development they still approach the human observer fairly closely, although not as closely as infant twos, but in this case appear very agitated, and give loud chitters and bob-and-bounce threats.

The variability of group behaviour in the presence of an observer was noted by Hall & Gartlan (1965). Later and more detailed investigations of this phenomenon indicated that those groups which reacted most strongly to the presence of an observer, were those with most juvenile males. During the second population survey on the north-west peninsula in June 1963, groups were classed either as "reactive" or "nonreactive" to the presence of the observer. The operational definitions of these two categories were as follows. Reactive meant that after contact with the group, chitters, chirrups or honks continued for at least thirty minutes, for at least three quarters of each minute, in the absence of movement from the observer. Non-reactive groups were those not reaching this criterion. Thirteen of the thirty-two groups counted reached this criterion, namely groups 4, 8, 14, 19, 21, 24, 26, 27, 28, 29, 30, 31,32. As several of the groups were counted in both surveys, those from the initial survey were discounted as they may have become habituated. Groups 1 to 7 were therefore dropped from the analysis. Twelve of the 25 remaining groups were reactive, and thirteen non-reactive. It was clear from watching these groups that the animals which began calling soonest and continued for longest, were the juvenile males, and it was clear from an inspection of the constitution of these groups that the more reactive ones were those with most juvenile males. In fact only one of them had only one juvenile male, whereas four of the non-reactive groups had only one, and one had none.

Plate 23. Infant two "investigating" observer. After inspecting the observer, often for considerable periods of time, the infants frequently perform this very characteristic posture, putting the head first on one side, and then on the other, and occasionally looking at him from upside down. The individual here was about to look from upside down.

The total numbers of animals in each group of "reactors" and "non-reactors" were noted, the analysis of age-sex categories was completed. On the basis of the total number of animals, and the fact that there were 25 groups, it was possible to construct the theoretical expected frequencies for both classifications. Thus, the observed number of juvenile males in the reactive groups was 33, whilst the expected number was 25, and the observed number in the "non-reactive" group was 20, whilst the expected number was 28. Chi-squares were then computed for each age-sex category, and for the total number of animals in each category. The observed and expected frequencies are given in Table 16..

The obtained values of Chi-square for these figures were for the adult males Chi-square = 0.5; adult females, Chi-square = 1.92; juvenile males, Chi-square = 4.85; juvenile females, Chi-square = 1.39; total, Chi-square = 4.40. The degree of freedom in all cases was 1. The required level of significance was .05%. The only two reaching this level of significance were the juvenile males and the total numbers. It must be concluded therefore, that the size of the group is important in determining whether the group reacts to the observer or not, but the social "catalyst" in this respect is the number of juvenile males present in the group. The data shown in Table 9 on group sizes and age-sex composition were analysed by means of a Spearman Rank Order Correlation Coefficient to determine the correlation between the number of juvenile males and the group size. The formula given in

TABLE 16

Analysis by age and sex categories of the observed and expected frequencies of animals in groups which were "reactive" to the observer, compared with groups which were "non - reactive".

	Reactive		Non-reactive	
	Observed	Expected	Observed	Expected
Adult males	39	36	36	39
Adult females	55	48	46	53
Juvenile males	33	25	20	28
Juvenile females	26	22	20	24
Group total*	169	150	144	162

* Group total is larger than the sum of the individual age-sex categories as infants are included.

Siegel (1965) p. 207, was used, as this incorporates a correction for ties. The obtained correlation was .76, the N was 25, only groups 8-32 being used, and the test was one-tailed as the direction of difference was predicted. The value obtained is significant at over the .01 level.

Thus the presence of juvenile males is likely to lead to this behaviour pattern in larger groups more frequently than in smaller ones as the larger groups tend to have more juvenile males. This observation provides a possible explanation of the adaptive significance of the larger groups observed towards the extremes of the geographical range. The result of large groups, with a consequently larger number of juvenile males would therefore result in groups which were more wary and difficult to approach, giving increased protection from potential predators than would be the case with smaller groups.

Adult males do not show either the interest in human observers exhibited by infant twos, nor the low threshhold for alarm shown by the juvenile males. The general reaction of adult males to the alarm chitters and chirrups of juveniles is to take little notice unless it is either very intense, or continues for a long period. Under these circumstances the adults move towards the source of the disturbance, the juvenile males, and look out towards the stimulus object. If this is not disturbing to them they move away silently and continue with their normal activities, if the stimulus is disturbing, they join in with honks (Plate 24).

The mean time of the appearance of an 'inspecting' adult male

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The mean time of the appearance of an 'inspecting' adult male

Plate 24. An adult male having had its attention drawn to a a disturbing stimulus by the chitters of the juvenile males, inspects the situation for himself, and considering it sufficiently disturbing, joins in with honks. These vocalisations are given to irritating or annoying stimuli rather than to dangerous ones, which evoke different calls with very different behavioural results.

after the onset of chittering of juvenile males for 34 observed incidents was 3.7 minutes. The range was from 18 seconds to 11 minutes.

In general terms, those signals which are both vocally and visually conspicuous are those associated with aggression, as they are directed at a disturbing stimulus, and provide information about the nature and movements of disturbing stimuli for other group members. There is probably also an intimidation function. Those behaviour patterns associated with fear, on the other hand are cryptic, and vocally and visually inconspicuous. They are directed towards avoiding the attention of potentially harmful objects in the environment.

It seems that although the signals have meaning in a social context, in that the whole group responds to them, they are responses of the individual without, so to speak, any social "intent". This was illustrated on several occasions when the observer was approaching members of a group who were sitting in a thicket about 50 yards away. On three of these occasions other members of the group were out in the grassland, only about ten yards from the observer, but hidden from him by an undulation in the grassland. On all three occasions the animals in the clump were watching the approach of the observer, but the distance was not enough to evoke fear or alarm in the group in question. But several members of the group were in "danger", being only a few yards from the observer and in the exposed grassland, yet no "warning" was given by those group members in the vegetation clump. Thus, when the observer reached the top of the undulation there were several members of the group in the grass only a few yards away. The adult male who was with them looked up first, gave the low frequency "cough oo" and the group dashed back to the shelter of the vegetation clump. This emphasises the point made by Lancaster (in press) that the vocalisations of non-human primates are emotional responses to the individual situation.

Visual investigation

The visual investigation of the environment is one of the main modes by which information about the state of the environment is obtained. Here it is proposed merely to describe those behaviour patterns of visual investigation which are apparently concerned with assessing the "suitability" of the environment, and which apparently have social significance.

During the day ranging, an animal that has filled its cheek pouches, or which has finished feeding for a short time, often then climbs into the high canopy cover and sits looking out over the surrounding environment whilst chewing or resting. Plate 25 shows AM5 of Group 1, who has just climbed into the high canopy and is looking out over the grassland.

This behaviour pattern seems in many ways similar to the "sentry" type of behaviour described by Hall (1960) for the chacma baboon, Papio ursinus. In that paper, whilst discarding terms such as "sentinel", "leader" and "guard", as carrying with them unjustifiable anthropomorphic overtones, Hall distinguished between incidental vigilance, dominant vigilance and undifferentiated vigilance. The same distinctions could not be made with the vervets of Lolui Island, but the relatively higher level of "irritability" of juvenile males has been mentioned, and this implies some social differentiation. But the calls by this age-sex category under these particular conditions are associated with threat rather than fear. Vocalisations indicative of fear and avoidance show a different pattern.

Plate 25. AM5 of Group 1, who during a pause in feeding has climbed to the high canopy and is looking out over the grassland.

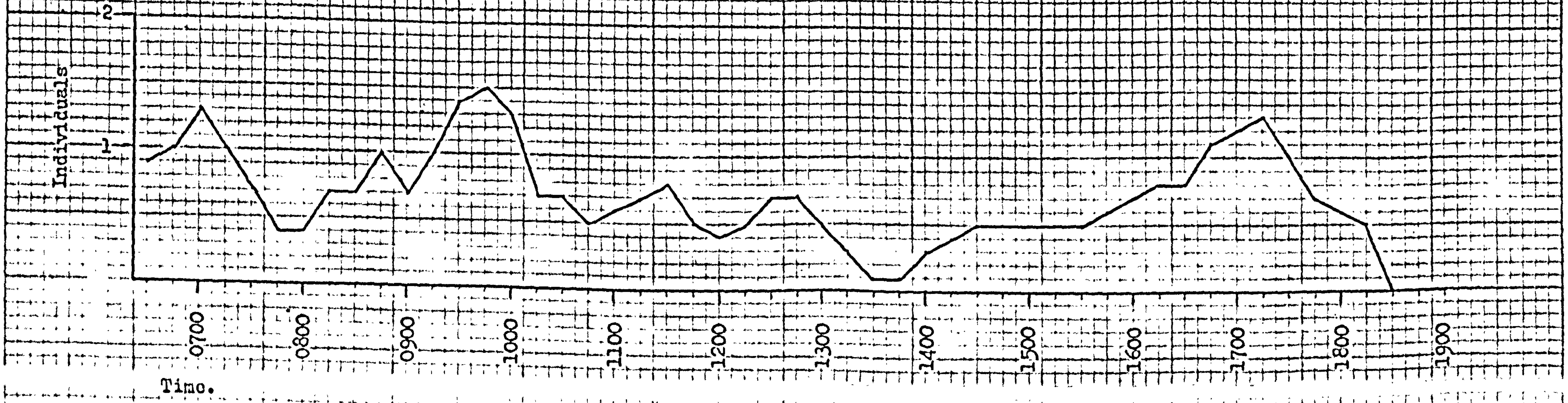
Animals of all age-sex classes perform the looking-out behaviour. It occurs throughout the day, but is especially common when feeding is at a high level. Fig. 23 indicates the mean number of individuals of Group 1 "looking out" at intervals of fifteen minutes, throughout the entire day, over five days. The curve is smoothed by a moving average of three. The pattern of the behaviour is distinctive; generally only one animal is engaged in this particular activity at any given time. It tends to be fairly high early in the morning and again in mid-morning, then declines until about 1400 hours, gradually increasing in frequency to a peak at 1730, then declines rapidly. The early morning peak is "looking out" that is performed before the animals have left their sleeping trees, and is a general inspection of the environment. The fairly high levels in mid-morning and the increase in the afternoon correspond to periods of movement, especially in the grassland (c.f. the pattern for grass ranging, Fig. 22). The lowest point at 1330 corresponds to the time when most animals are either resting or feeding on the inside of the vegetation clumps. The salient point, however, is that it is a minority activity, being performed by very few animals at any given time, with the peaks largely coinciding with periods of movement both in the thickets and in the grassland. The mean number of animals engaged in this activity for each 15 minute interval throughout the five days was .72.

All age-sex classes except infant ones performed this activity, but there were important variations in the frequency with which the different age- sex classes performed it. The total observed

Fig. 23

Mean number of individuals "looking out" per 15 minute period over 5 days, May 1964.

(Curve smoothed by moving average of 3)



instances of the behaviour pattern over the five days was 172. The observed frequencies of the different age-sex classes and the expected frequencies, based on an equal division of total observed frequencies between all individuals are shown in Table 17.

A Chi-square test (Siegel, loc.cit.) on the data shown in Table 17 gave a value of Chi-square = 82.01, and with 5 degrees of freedom, this value was significant at over .001% level of confidence. The main variations from the expected frequencies accounting for this result are that adult males perform it much more than expected, and infant twos much less than expected. It is likely, however, that the infant twos were only in the process of learning this behaviour pattern, and in fact in many cases accompanied their mothers when the latter were engaged in the behaviour (Plate 26). In order to minimise the effect of the low figures for the infant two category, a second Chi-square was calculated with the incidents involving them and the age-sex category dropped from the analysis. For these data the expected frequencies are, AM, 32.55; AF, 65.10; JM,10.58; SF, 21.7; JF, 21.7. The only age-sex class which has an expected frequency similar to the observed one is that of adult females. Adult males were observed engaged in looking-out almost twice as often as theoretically expected, juvenile males only half as frequently as expected, sub-adult females half as frequently as expected, and juvenile females only about one third of the theoretically expected figure. The calculated value of Chi-square for this figure was 43.08,

TABLE 17

Total observed and expected frequencies of "looking-out" by age and sex classes, Group 1, May 1964.

Age-sex class	No. in group	Observed frequency	Expected frequency
AM	3	61	25.8
AF	6	68	51.6
JM	1	5	8.6
SF	2	10	17.2
JF	2	8	17.2
I2	6	20	51.6

and there are four degrees of freedom. This value also was significant at over .001% level of confidence.

It is from the "look-out" position that the alarm call that has the greatest social significance is given most frequently. This is the "soft alarm call", it is a low-frequency vocalisation, rrr --- rrr --- rrr repeated several times. At the sound of this call animals immediately descend to the undergrowth, or if they are in grassland dash for shelter to the nearest thicket. The animals then remain motionless in the vegetation, and there is no further vocalisation until the danger is past. Of 58 soft alarm calls (sac's) heard during the last three months of study, 48 of them were given from the looking-out position, one was given from an anthill, and nine were given by animals which were not visible to the observer.

It seems, therefore, that adult males play a particularly prominent role in this vigilance behaviour. Females play a relatively minor role in the juvenile stage, the frequency of the behaviour increasing as the individual becomes subadult, and reaches the maximum frequency in adulthood. The same applies to males. The mechanics of the behaviour are not understood as yet. It can be seen from Fig. 23 that it is comparatively rare for more than one animal to be involved in this activity. Yet it does not seem to be organised in any way according to "rules" or "traditions". It seems possible that the stimulus for an animal to cease "looking-out" may be the appearance of another animal engaged in the same behaviour.

It is interesting to note that in view of the high level of chittering already noted in juvenile males, there was less than expected of this "looking-out" vigilance behaviour in this age-sex category. It must be assumed, therefore that the defence and alarm mechanisms of the group are differentiated according to age-sex classes. Threat and aggression towards intruders, which would normally be towards members of the same species, or non-dangerous but annoying intruders, is the province of juvenile males, whereas the inspection of territory and serious aggression against intruders is the province mainly of adult males, although adult females because of their superior numbers in this particular group played a similarly important role in the vigilance behaviour of the group.

Plate 26. Adult female who is "looking-out" is joined by her infant two. The photograph shows the infant about to mouth her.

Grassland ranging is an activity which exposes the individuals to a higher degree of danger than is generally the case in the forest and thickets. They are, as has been noted, less confident in the grass and never threaten the human observer from there, but run to the security of the nearest vegetation cover as a base from which to threaten. It is partly for this reason that there is so much sitting on exposed rocks and termite mounds, with consequent deposition of faeces in these places. Anthill and rock looking out was in many respects similar to "looking-out" in forest and thicket, and showed the same characteristics, with the main difference that when a group was out in grassland an individual looking out on an anthill or rock was almost invariably present.

If an animal out in grass was disturbed by anything moving or any unfamiliar object, the general reaction was to stand on the hind legs and inspect it from a standing, bipedal, position. (Plate 27). This position is only adopted in mildly stressful situations, and if the source of the disturbance proves to be in fact a potential danger, the general reaction, especially of males, is then to move the arms upwards and sideways, so exposing suddenly the bright white fur of the chest. This is distinct for the "bob and bounce" threat in that the bob does not appear; the intimidation part of the display is however probably homologous. Both these positions have social significance, in that if an animal observes another in the bipedal stance, it then tends to adopt the same stance, and look at the disturbing object. This behaviour pattern begins to appear by the second month of life.

Plate 27. Juvenile male standing and inspecting an unfamiliar object in the grassland, an egg box, about 12 metres away from where the animal is standing.

LOCOMOTION AND POSTURES

Jolly (1964) states that by anatomical criteria, C. aethiops is neither a strictly arboreal nor a terrestrial animal. This hypothesis is borne out from the Lolui data, specifically the amount of time spent on the ground and in trees (c.f. Fig. 22). In his analysis of locomotory patterns leading to his conclusion, Jolly distinguished between three typical positions of the hand used in locomotion, and two positions of the feet. This catalogue is as follows:

1. Hand positions

   a) Digitigrade. The whole palm is not applied to the surface, the body weight being borne upon the volar surfaces of the fingers and the pads lying over the metacarpal heads only. Little or no weight is borne on the pollex, the tip of which normally reaches just to the ground. The wrist is therefore held so that the carpals and metacarpals are in line with the long axis of the forearm, and there is marked hyperextension of the metacarpal-phalangeal joint. This position is typical of ground locomotion.

b) Plantigrade. The whole of the volar surface of the digits and palms is applied to the surface; in this case the outside and upper surface of the branch, most of the weight appearing to be transmitted through the thenar eminence. This position is typical of branch walking.

c) Plantigrade, modified. Closely resembles the plantigrade position used in branch walking, the only difference in position being the greater pronation of the forearm (if the fingers point forward) and the greater hyperextension of the wrist. Unlike a branch, a flat surface cannot be passed between pollex and index, so the fulcrumation must occur at the wrist rather than between thumb and index finger.

2. Feet positions

a) Simple plantigrade. The feet is placed flat on the ground, not everted, and without marked abduction of the hallux, which has no special function in opposing the rest if the digits as it has in branch-standing. Typical of ground standing and walking.

b) Hallux-gripping. The position of the feet is slightly inverted so that the sole faces slightly medially. The whole of the volar surface of the sole and of the digits is applied to the surface of the branch, and the hallux being widely abducted and applied so that its volar surface and that of the hallucal pad and web is applied to the upper and inner surfaces.

In an analysis of the foot and hand positions of the species in the London and Paris zoos, four specimens in the former case, two in the latter, Jolly noted a difference in the hand position in ground walking of the two populations. Whereas the London specimens used the efficient digitigrade method, the Paris individuals used the plantigrade on the ground. This habit is typical of exclusively arboreal Cercopithecus species, such as C.diana, and perhaps indicates that the French specimens, originating probably from former French territory in West Africa, may be more strictly arboreal and forest-dwelling than is the case in East Africa.

In branch-walking the Lolui population used the plantigrade habit of the hands, and the hallux-gripping habit of the feet (Plate 28). This position is observed only when the opposition of thumb and digits over the branch is possible. When the dimensions of the branch are such to prevent this, the modified plantigrade method is typically adopted. However, the number of branches of these larger dimensions is not great outside the fringe forests, and consequently this method of progression is not commonly seen in thickets and vegetation clumps.

If the opposition of thumb and digits is possible this is typically used in ascending into trees and shrubs. Descending is also by this method if possible, and in both cases the head faces the direction of movement. The ascending of thick trunks, and to some extent the descent of these same obstacles seems to present some difficulty in obtaining purchase against the almost vertical face.

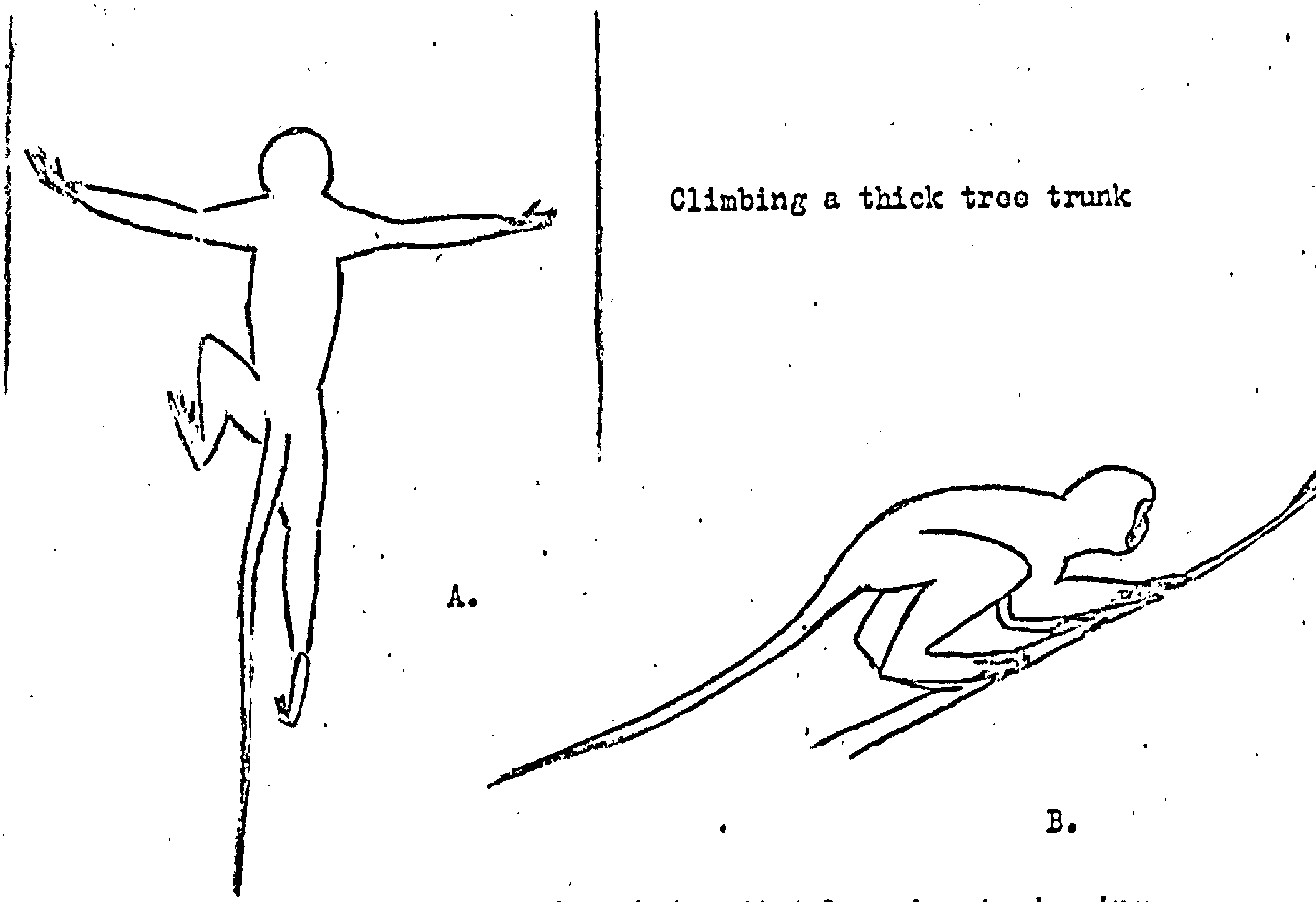
Plate 28 Typical hand and feet positions in branch-walking. Note opposition of thumb on both hand and feet.

The general method of solving this problem, for the ascending of trunks is for the arm to be outstretched, at right angles to the spinal axis, to enable the fingers to obtain some grip against the side of the trunk. The arms are then moved up simultaneously, the feet are moved alternately and provide the upward impetus, the arms and fingers providing a brake to prevent slipping between the alternate foot movements (Fig. 24A). If the trunk is of a small enough diameter to permit, the arms may encircle it almost completely. The feet and hand movements are the same as in the previous case.

The descent of thick vertical trunks presents even more difficult problems. The basic method is essentially the same as in Fig. 24A, but in reverse, the arms are outstretched in the same manner with the fingers used as a brake. The feet are either used alternately, or rarely, together in little hopping movements. The descent is tail first, and the animal often looks round and down at the ground whilst engaged in this method. The last few feet are often dropped straight to the ground or a convenient branch. If the descent is hasty, an attempt is sometimes made to descend head first, although usually only on trunks with a slight angle. This is generally only successful for the first few feet, after which the animal swings round and descends in the orthodox tail-first manner.

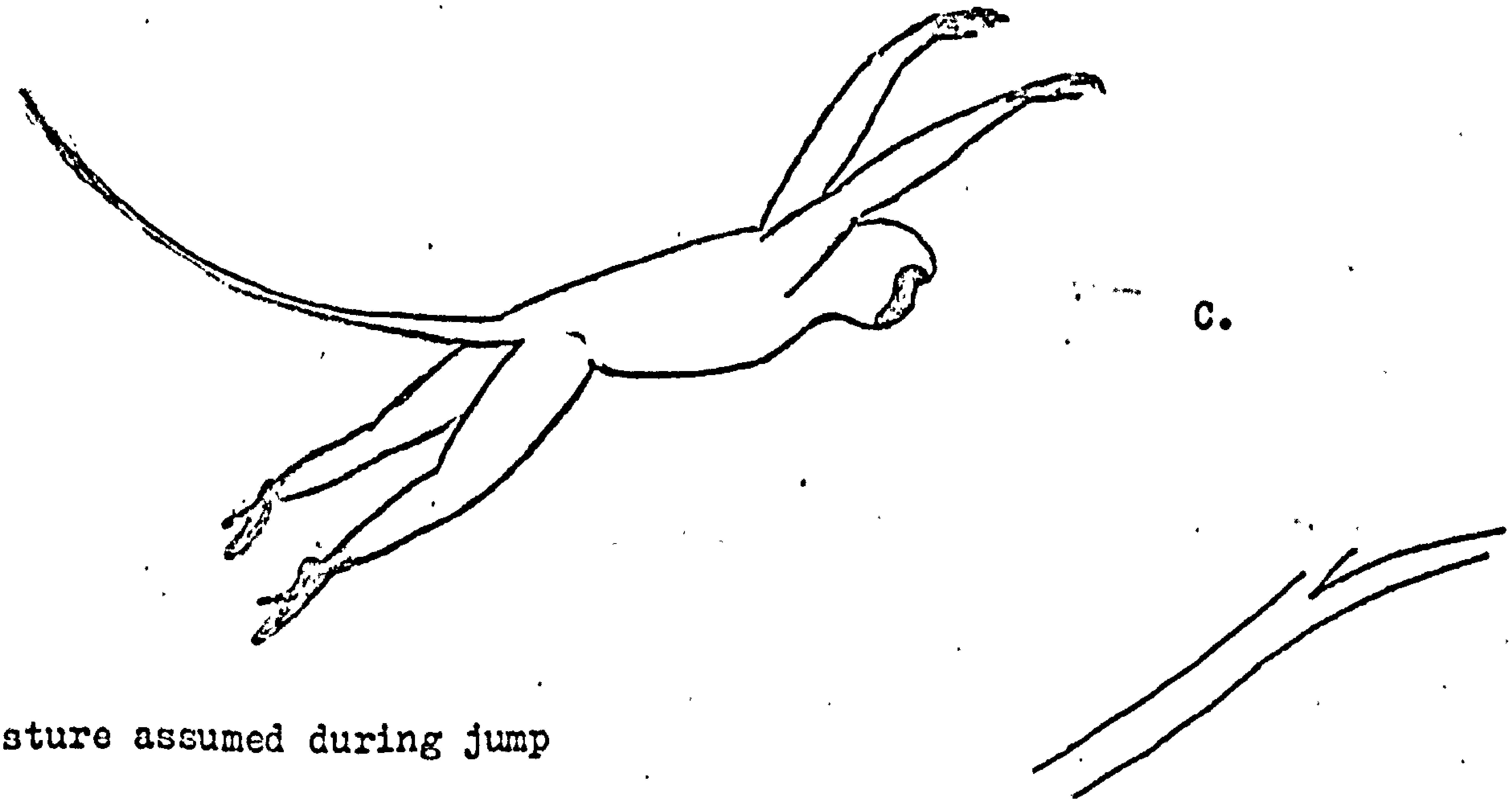
Jumping from branch to branch and from tree to tree is a very common behaviour pattern, and used frequently in the day range. The jumps are generally made from the shortest distance

Fig. 24



Climbing a thick tree trunk

Crouch immediately prior to jumping



Posture assumed during jump

between the two points, and therefore often involve jumping between relatively thin branches. The pre-jump posture is very characteristic (Fig. 24B) and jump-intention movements may be made for several seconds before actual take-off. The actual jump posture itself (Fig. 24C) is very characteristic; the arms are outstretched upwards and forward, the legs extended backwards, the tail out behind, and this is frequently whirled round in a flailing motion during jumps, especially those which are exceptionally long. The tail is an extremely important organ for the maintenance of balance in this species. In general it may be stated that the faster the movement in the trees, the more use is made of the tail. The angle of the body assumed during jumps varies between almost horizontal and an angle of about 45^{o}, depending largely on the position of the landing point in relation to the take off point.

The transition from grassland to a vegetation thicket, or vice versa is generally accomplished by means of a jump rather than climbing. The distance jumped down is generally about three or four feet, and that jumped up about two to three feet.

No movement similar to any brachiation movement was ever seen in the Lolui population, and swinging by the arms from a branch was only seen in infant twos, characteristically in their play-groups, and occasionally in juvenile animals.

Accidents resulting in falls are not uncommon, and arise from two main causes. Firstly the fracture of thin or brittle branches particularly of Canarium schweinfurthii, under the weight of animals, or from misjudgements of distance by jumping animals, or to a combination of both.

The commonest cause of falls was the result of a combination of these two factors encountered in the territorial display known as "jumping around", which is described in more detail in the section on territorial behaviour. Falls of twenty-five feet or more were not uncommon, and the largest was of approximately sixty feet. No animal was ever seen injured as a result of falling.

It is difficult to estimate the comparative efficiency of the species in their utilisation of trees, as very little data exists on the number of falls or accidents in other species. The mean number of falls, which included those arising both from misjudgements and from fracture of branches, in Group 1, for six months of study, gave a mean for the group of 1.3 falls per day. The only comparable data seems to be that of Washburn (pers. comm.) on the incidence of fractures in skeletons of Hylobates sp. Washburn states that as many as 75% of animals have at some time suffered from fractures. This would suggest, as a first approximation, that C.aethiops is at least as efficient in this sense in the utilisation of the tree storey of the environment as is the Gibbon, and probably considerably more so.

Normal ground-walking of the Lolui population of C.aethiops was quadrupedal. The position of the hand in all animals it was possible to see was digitigrade, and that of the feet simple plantigrade. This is what would be expected from a population that spends such a large amount of time on the ground. In normal walking the diagonally opposite limbs are moved synchronously, left leg and right foot being moved forward simultaneously, followed by right leg and left foot. This is basic day ranging walking. If speed is increased slightly, the same limb sequence is seen. However, as speed increases the sequence changes, and the fore-limbs and hind-limbs are moved together in sequence. This is the gallop, and is used both in the normal day ranges when it is important to avoid another animal, or move to another food source fairly quickly, or it is used in escape and rapid avoidance.

Very occasionally, bipedal locomotion is observed in grassland, generally when the hands are occupied with an object. It is seen most commonly when adult females pick up an infant and start to move off, the first two or three steps then are commonly bipedal. The same also occurs when a large fruit such as _Saba florida_ is being held in the hands, and the animal takes it to another location, such as a rock in order to eat it. The sequence in which the limbs are moved in this case is also alternate. On two occasions, however, animals were disturbed by the observer in grassland with _Saba_ fruits, one an adult male, one an adult female, and in both these cases the fruit was not dropped, but the animal in trying to reach thicket cover as quickly as possible, adopted the bipedal stance, but moved both hind-limbs simultaneously, in a series of kangaroo-like hops. The adult male moved fifteen yards in this manner, the female only four.

In normal walking in the grass on Lolui the tail is held horizontally to the ground, or drooping towards the ground, at an angle to the body. This was not the case with Starck and Frick's population nor with the population observed by the author at Chobi in northern Uganda. In these two latter cases it was common for the tail to be held vertical, at least at the start of the movement, or slightly curled up over the back. The Lolui population retained the capacity for this posture, and it was commonly seen in agonistic encounters, but never in the normal day-ranges. The most likely explanation for this difference seems to be that the usual low-frequency grunts given in grassland, and which presumably promote group cohesion, are not functional at long distances, and as such distances are necessary at Chobi because of the impoverished nature of the environment, the vertical position of the tail at the beginning of a movement serves as a signal of the position of the animal and the direction in which it is travelling to the other members of the group. Such signals are apparently not necessary in the small territories of Lolui Island.

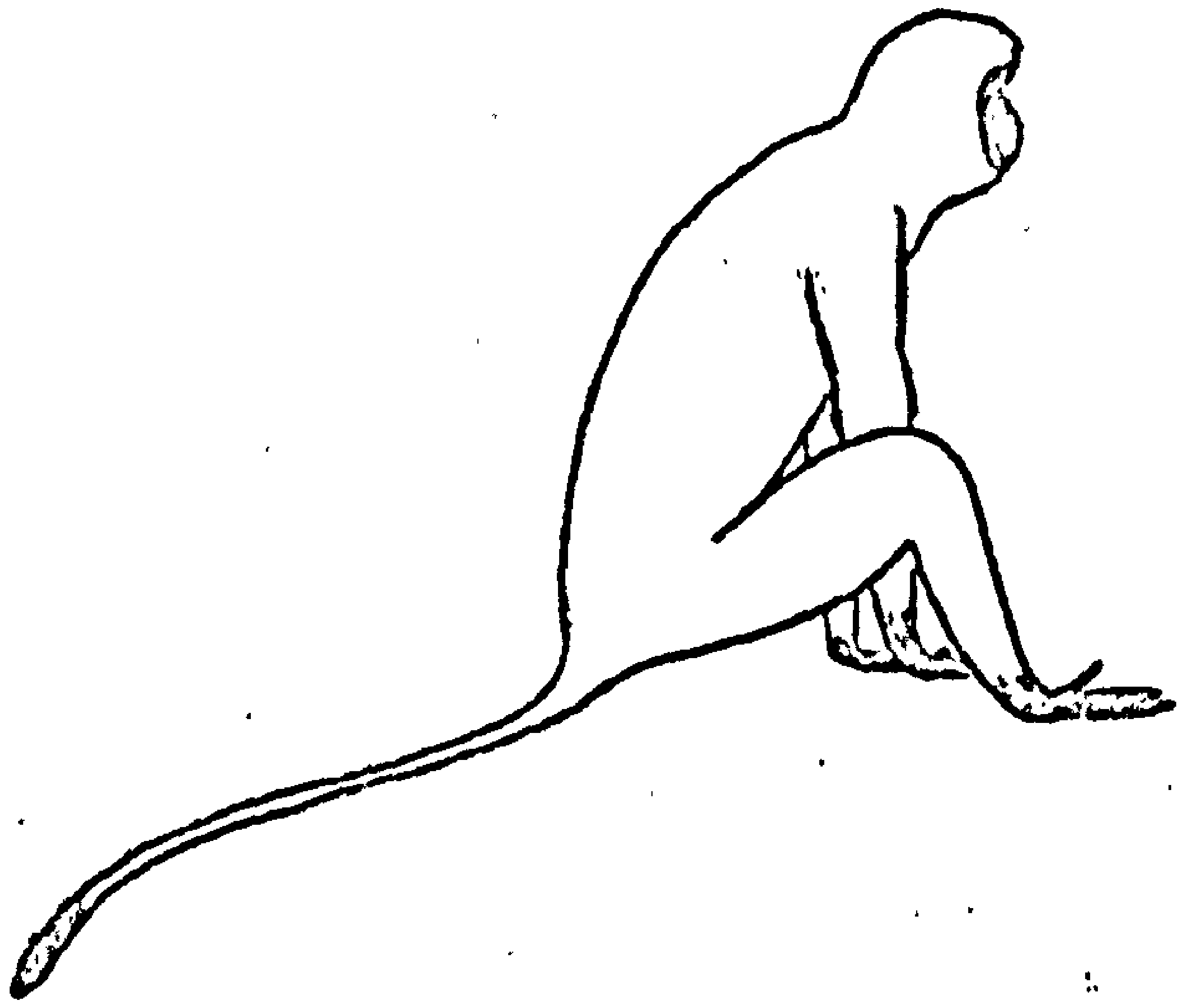
The locomotory patterns so far described are common to all age and sex classes, except where there are maturational differences, and these have been described. No differences were observed in the frequencies of occurrence of the different patterns in age sex classes, except for falls, which were more common amongst males than females. There were two main reasons for this. Firstly, adult females with infants usually did not jump from tree to tree, and secondly, the "jumping around" territorial display which often led to falls was an adult male activity. These two factors combined explain the observed difference of 41 falls being of males, and 24 of females in Group 1 in spite of the fact that the ratio of males to females in this group was approximately 1:2 throughout the year.

Common resting positions also showed no age-sex differences, once infants had become independent of the mother the usual adult patterns of resting postures were observed in the infants. The typical resting posture in trees was shown in Plate 21. The back is curved, the tail hangs loose, and may be curled round the trunk or branch at right angles to the branch on which the animal is resting. The head is not low on the chest, as is usual in the sleeping posture, but is generally held so that the eyes look straight ahead. The knees are drawn up towards the body, but are generally apart, the feet holding onto the branch, the arms may be either inside or outside the knees, the hands resting on the branch just in front of the feet. (Fig. 25A).

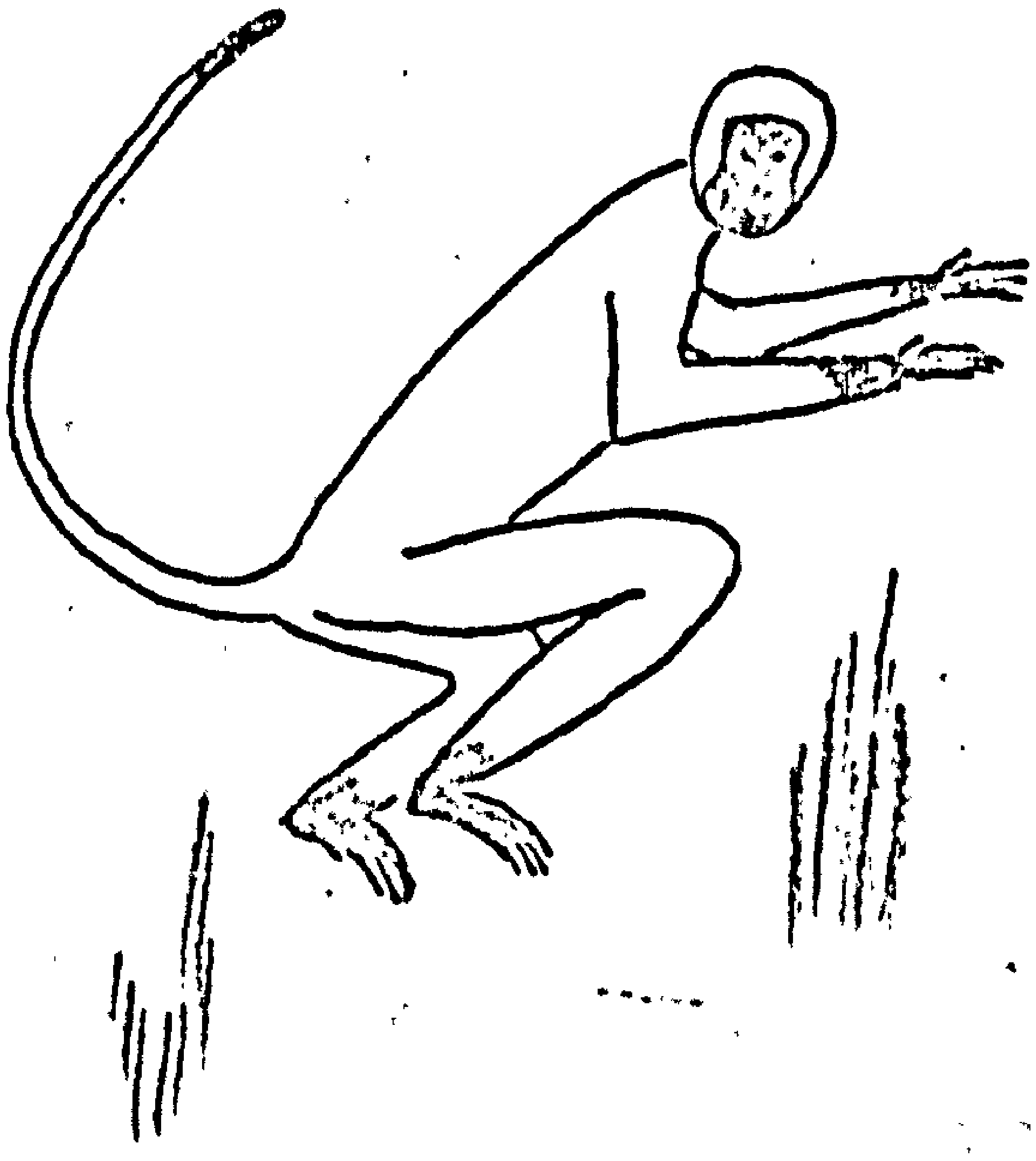
The same posture is generally assumed in resting on the ground or on anthills, but the feet are generally flat as they are not used in gripping. Occasionally, when the sun is hot animals will lie on their sides or back on rocks or termite mounds in the sun. This is common in grooming, but not common as a resting posture.

Another posture that is occasionally seen in grassland, but which is comparatively rare is the "gallop leap". When an animal, either male or female has been disturbed by an intruder

Fig. 25



A. Typical relaxed sitting position



B.

"Gallop-leap" by animal running away in grassland, with glance at source of disturbance.

in the grassland, or has been alerted by sac's of another animal, it gallops to the nearest cover, but in the course of this gallop often executes a leap, by breaking the rhythm of the stride and taking two successive steps with the hind limbs. This generally brings the animal into a vertical position, from which it looks round momentarily at the source of the disturbance. (Fig. 25B).

"Displacement" scratching, and the rubbing of the nose with the back of the hand are very common activities observed in approach-avoidance conflict situations, as were urination and defaecation and yawning, or gaping. These behaviours appear in all age-sex classes except yawning, which appeared to be exclusively a male activity. (Table 18). Threat postures, however, were subject to differences in frequency of appearance according to age and sex, as would be expected from the previous data on social differentiation within the Lolui groups. Records for subadult females are considered here in the adult category for the purpose of these calculations.

Two of these behaviour patterns were only observed during the first two study periods, namely displacement mounting and yawning. Table 18 includes data from population surveys and infant counts, and from the more detailed studies of the groups on the north-west peninsula, which were giving virtually no threats towards the observer at the end of the study, and then only in exceptional circumstances, such as when suddenly disturbed in grassland.

TABLE 18

Total observed frequencies of certain threat postures and displacement activities from groups of the north-west peninsula.

Behaviour pattern	Age-sex category			
	AM	AF	JM	JF
Scratching and nose rubbing	173	468	229	194
Displacement aggression and mounting	32	16	9	3
Yawning (threat)	22		5	
Urination and defaecation	30	40	32	18
Bob-and-bounce threat	84	44	112	32
Sit-threat	10	55	82	13

Whereas urination was a fairly common fear-response and observed throughout the study, defaecation and urination simultaneously seemed to indicate a greater level of fear, and were only observed in simultaneous combination during the first joint survey of the island.

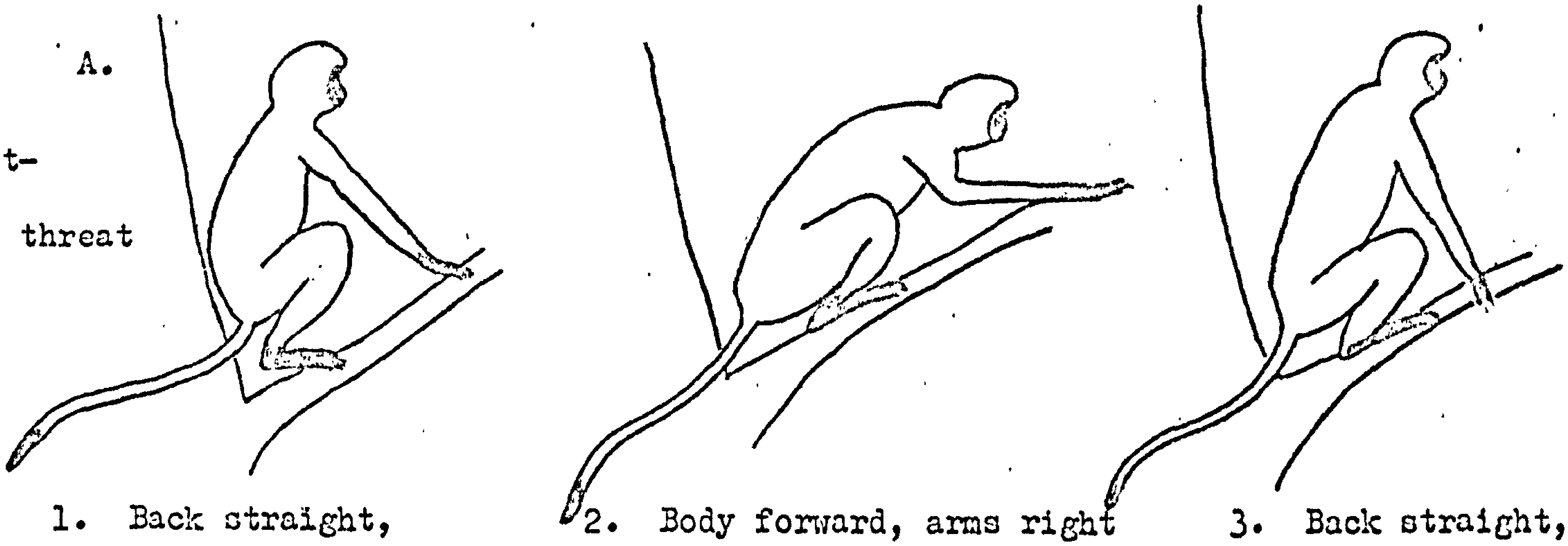
The sit-threat is a sequence of movements involving head, shoulders and limbs. The animal generally sits with arms stretched out in front of it, holding onto a branch. The upper part of the body is moved suddenly forward in the direction of the disturbing stimulus, so that the arms are moved forward along the branch. In this position the head and shoulders may be moved laterally, in a side-to-side jerking motion. This may also occur in the upright position. The eyes are fixated on the eliciting stimulus throughout the movement. The body is then moved suddenly back to the upright position, with the arms either straight out, as at the beginning of the movement, or down about 45° from the body line and 90° from each other (Fig. 26A).

The bob-and-bounce threat (Fig. 26B) was performed either in trees or on the ground. In trees it was executed from a quadrupedal position; firstly the head was lowered with a rapid bobbing movement which was generally accompanied by the raising of the eyebrows and the consequent exposure of the white eyelids, if present. It is similar in this respect to the "threat face". The bob is followed by a crouch, the hind legs remain fully extended, the arms are fully extended laterally, the chest almost resting on the

Fig. 26

A.

Sit-threat

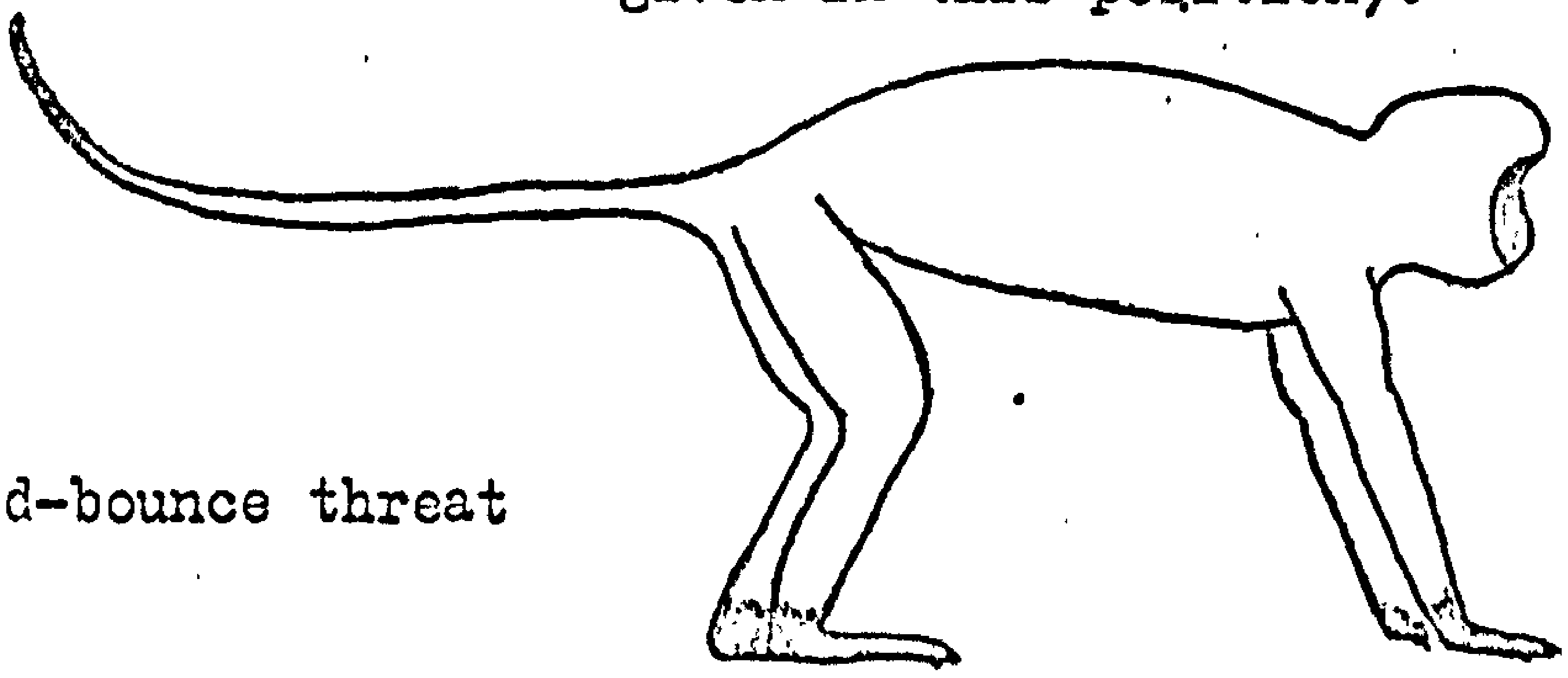


1. Back straight, arms forward.

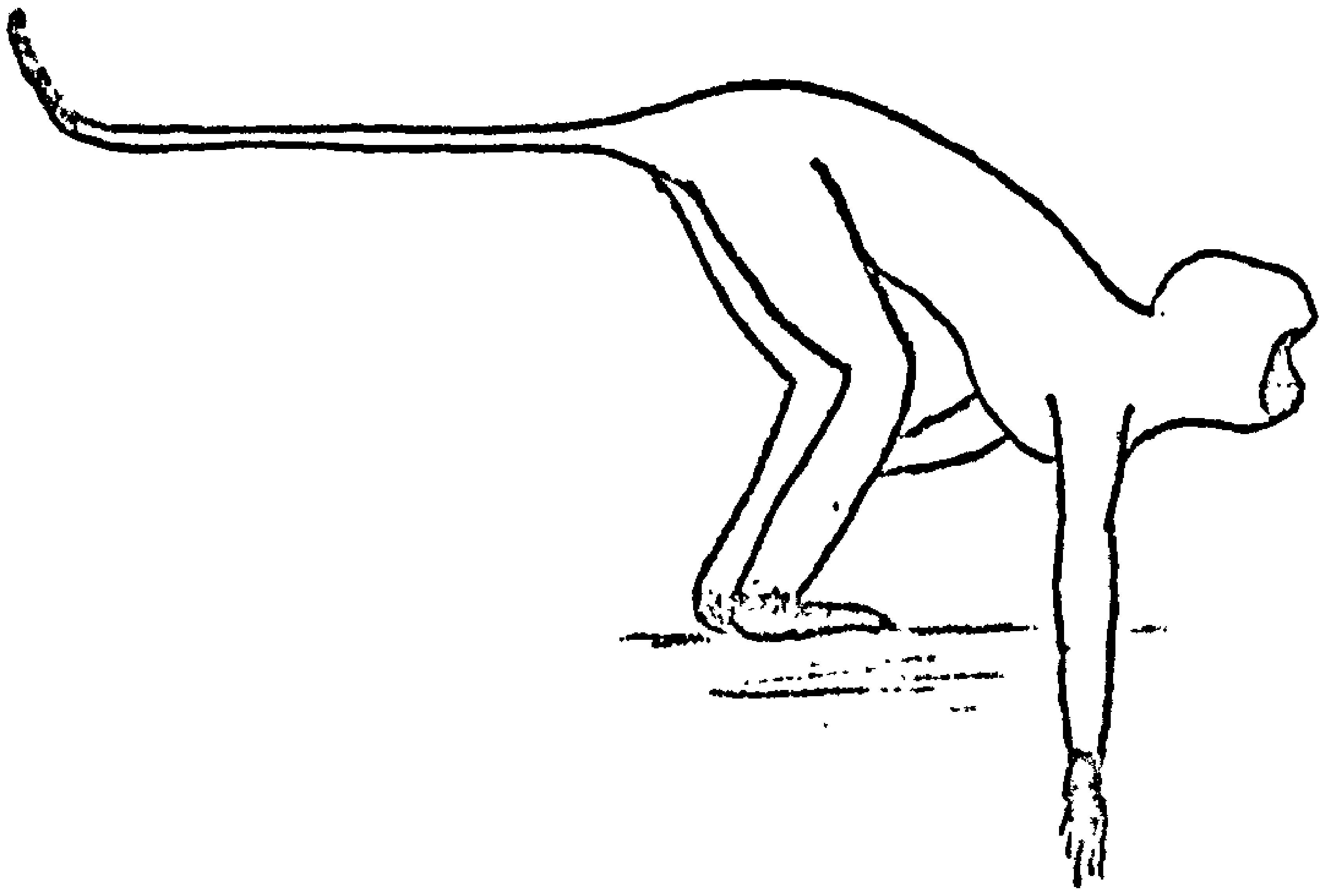
2. Body forward, arms right forward. (Lateral movements given in this position).

3. Back straight, arms down.

B. Bob-and-bounce threat



1. Head bob.



2. Crouch down from bob position, hind legs straight. Leading to bounce to bipedal stance with arms outstretched, then back to position 1.

branch. This posture may be held for a second or two, and is followed by a sudden bounce upward, the arms are flung up and outward, the body is moved back and upwards, the hind legs remain fully extended. The white fur of the chest is suddenly exposed in this posture. This latter component is also occasionally seen at the end of a "bipedal inspection" in grassland.

The threat posture described by Hall and Gartlan (1965) as Type 2, "bouncing on branches or bushes" was in fact not a threat posture at all in the present sense. It is a territorial display, and the reason for its appearance under the circumstances of the first trip was that the appearance of the two observers caused such panic that occasionally animals crossed into different territories, causing the jumping-around display to be elicited. The display will be considered in detail in the section on territorial behaviour, but is not considered here as a threat posture.

Urination and penile erection in males was extremely common under even relatively low levels of excitement. Urination and simultaneous defaecation were, as has been mentioned, only observed in the first study period and must therefore be considered as examples of extreme excitement. Although the observer entering vegetation clumps at this time was often showered with urine and faeces, there was no evidence that this was "deliberate" or "directed". The tendency of infant twos to come close and inspect, and that of juvenile males to come close and chitter has been mentioned, and the results were incidental.

Yawning which occurred when groups were habituated and which, from situational evidence, was likely to indicate tiredness on behalf of the animal concerned was excluded from Table 18, and all age-sex classes were observed to carry out this behaviour. The distinction between "tired" and "displacement" yawns is not always easily drawn, and doubtful cases were included in "tired" yawning rather than in "displacement" yawning. This latter behaviour also was only observed during the first two study periods, and must also therefore be taken as indicative of exceptional social stress rather than as a normal part of the behaviour repertoire.

Although Hall, in Hall & Gartlan (1965) recorded three instances of "twig-breaking and dropping", the present author never observed any incident which could with confidence be ascribed to this behaviour category. The extremely brittle nature of dead branches of Canarium schweinfurthii, however, ensure that if a bob-and-bounce threat is carried out, almost certainly fragments of twig will be broken off and drop to the gpund in the vicinity of the observer.

Displacement mounting, which was seen seven times in adult males and twice in juvenile males was also only observed during the first two study periods, and was also therefore indicative of rather extreme social stresses. Displaced aggression, however, was often observed, but was most common in groups that had not been completely habituated to the observer when they were approached.

On eight occasions individuals in Group 1, having been deprived of a food item by accidentally dropping it, came and threat-faced the observer, and on five occasions gave mild threat chitters.

Scratching and nose-rubbing was the displacement activity with the lowest threshold. It occurred in all types of situations where there was the slightest amount of frustration or conflict of motives. Scratching was either of the body with either hands or feet, or of one limb with a hand. Nose-rubbing was usually with the back of the hand, and involved three or four wipes.

The figures for "bob-and-bounce" threat postures, and those for "sit-threats" shown in Table 18 were analysed by means of a Chi-square test to determine whether the observed frequencies in the different age and sex classes were significantly different. The observed frequencies were those indicated in the table. The expected frequencies were based on the total population structure obtained from the survey of the north-west peninsula, (Table 9). The expected frequencies thus obtained for the "bob-and-bounce" threat were AM, 73; AF, 98; JM, 49; and JF, 49.

The Chi-square value for these data was calculated as 118.00. There are three degrees of freedom and this value is significant at over the .001% level of confidence. The main causes of the differences are due to the fact that this behaviour pattern is performed much more often than would be expected by adult females and juvenile males. The figures for adult males and juvenile females were similar to those expected.

The expected values for the sit-threat were AM, 43; AF, 58; JM, 29; JF, 29. The calculated value of Chi-square for these data was 210.50. There were three degrees of freedom, and this value was also significant at well over .001% level of significance. The causes of the difference here were that adult males perform this behaviour much less than expected, as do juvenile females. Adult females perform slightly less than expected, but juvenile males perform it almost three times as often as theoretically expected.

The conclusions to be drawn from these data are similar to those from the vigilance and alarm data, namely that there is a considerable amount of social differentiation. "Bob-and-bounce" threats, which appear to be a higher threshold threat than the "sit-threat", are performed more frequently than expected by the females and the juvenile males.

The "sit-threat" on the other hand, which is a rather low-threshold threat, is performed more by juvenile males than by all other age-sex groups combined. This agrees with the higher irritability of this age-sex class demonstrated in the alarm call data.

In conclusion to this section, it may be stated that perhaps the most important finding was of the differential use to the group of the different age-sex classes. Juveniles and infants are not merely the "wards" of the group until they reach adulthood, but the group has a differentiation and different roles which are based on the age-sex structure.

SOCIAL BEHAVIOUR.

COMMUNICATION

Before starting any discussion or description of the communication patterns and behaviour used by the Lolui population, it seems important to state exactly what is meant by this term. Marler (1965) stated that the characteristics of communication behaviour were that it is "initiated by one animal, which produces the communicatory signal, mediated by the environment through which the signal is transmitted, and culminating in the response evoked by the signal in a recipient." This definition is unexceptionable, but it raises the problem of the motivation of this behaviour, and the extent to which it may be considered as "purposive" or socially motivated.

Evidence has already been given indicating that members of a group who were in danger and yet unaware of it, were not warned of the danger by other members of the group who were themselves not in danger, although the latter had perceived the approaching stimulus. This would tend to indicate that what is termed communication is in fact an individual response to some aspect of the environment, which has a signal value to other members of the group, but which is not given with the "aim" of alerting the other members of the group. It is an individual, not an altruistic response.

In view of the fact that what is communicated is an individual emotional response to some aspect of the environment, it may be hypothesised that individual variations, learning and environmental differences all combine to effect differences in the frequency with which different vocal patterns appear, their intensity, and local variations in structure. Struhsaker (pers. comm.) in a study of C.aethiops in the Masai Amboseli Game Reserve, Kenya, concluded that in that population there were thirty-six distinct vocal signals. Even allowing for differences in classification and terminology between the two studies, so that certain patterns which Struhsaker considered as vocal signals, such as vomiting and hiccuping were excluded from the Lolui list as being of doubtful signal value or social significance, there is still apparently a large real difference in vocal repertoire between the two populations. Vocalisations occurred at Amboseli which were not heard on Lolui, and the same applied to social postures and vice-versa.

At Amboseli there was a distinct alarm call for snakes, which has a great social effect, and yet was not heard on Lolui; the reaction of this population to snakes has already been described. There was also a distinct call for aerial predators at Amboseli which was not heard on Lolui, presumably because of the absence of this environmental hazard. Social postures were described at Amboseli which did not occur on Lolui, and the scent-marking of territory observed on Lolui was not observed as part of the social repertoire at Amboseli.

The types and frequencies of different vocalisations and social postures can therefore be expected to provide a reliable and quantitative guide to the relationship of the population with the environment. This is certainly true of intra-species comparisons, and may even provide a basis for inter-specific or even inter-generic comparisons.

The unsatisfactory tape recorder used in this study, combined with the lack of servicing and repair facilities in Uganda, resulted in no recording of a sufficiently high standard for spectographic analysis being made. It was also a drawback in another respect; whereas the common vocalisations are soon recognised, the rare ones are often difficult to remember, or to transcribe effectively, and there is no reliable means of comparing those which appear only once or twice a month. The analysis of calls made in the remainder of this section is based on field notes only, in which combinations of alphabetic sounds were used to describe the different vocalisations.

The terminology used in this section is that proposed by Andrew (1963), as follows.

1. Noise is used of vocalisation with no tonal structure, sound of vocalisation with an obvious fundamental and overtones.
2. An "arr" call is composed of rapidly repeated narrow columns of relatively faint noise; a "ha" is a single such column.
3. A "cluck" is a narrow column of sound with a superimposed high pitched fundamental and overtones. A titter is a bout of soft clucks.

4. A "grunt" is a deep sound with little noise.
5. A sharp call is a fairly narrow column of intense noise with no marked concentration at any frequency level.
6. A "shriek" is a loud call with much noise and a high broadened fundamental, or a concentration of noise representing such a fundamental. A "yip" is a call made up of a short segment of a shriek.

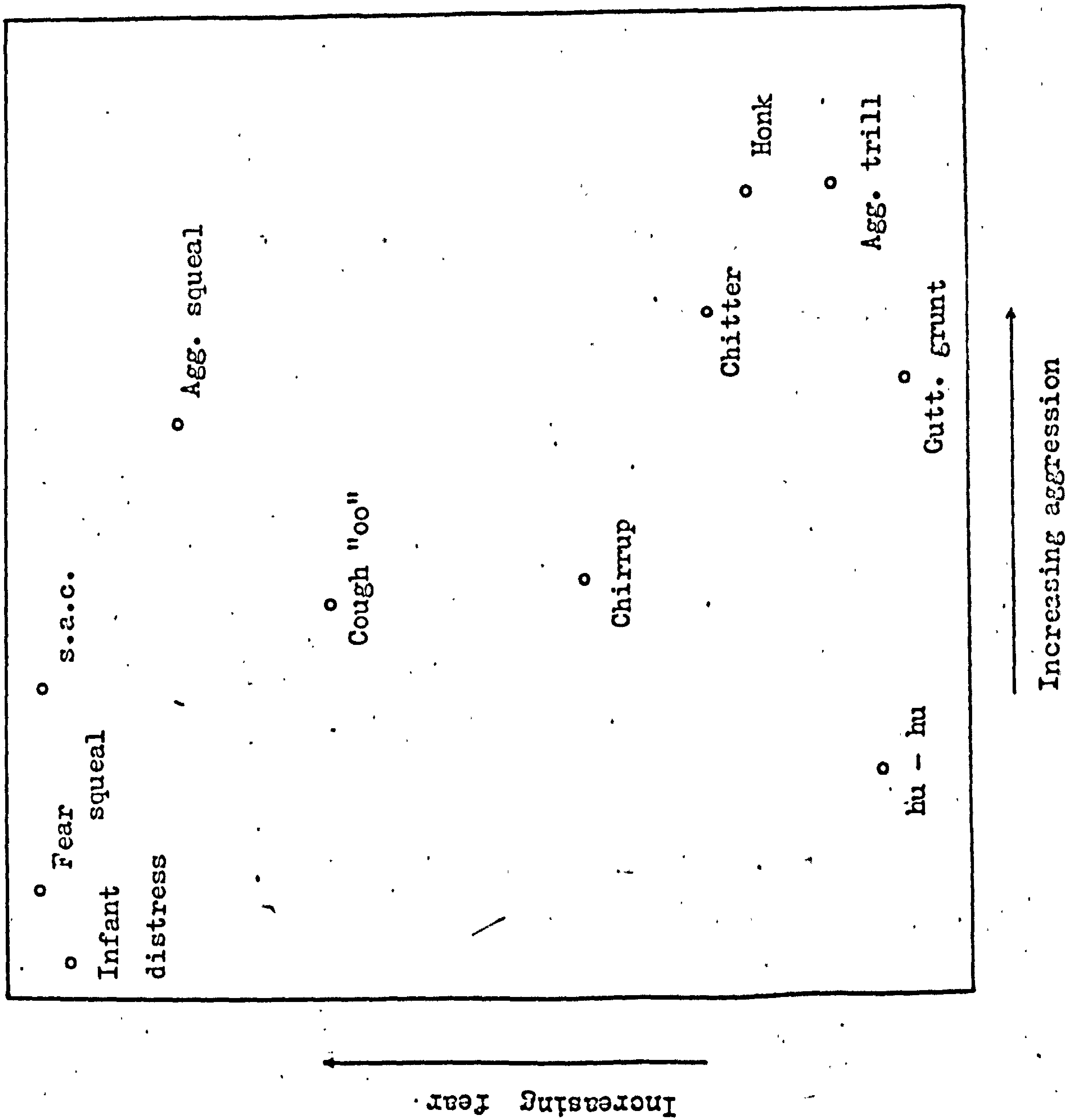
The majority of calls are those associated with aggression or fear, and these are shown in Fig. 27, together with the gradations between the extremes, and the relations between the different vocalisations. Firstly, however, all calls which were heard in the field and considered distinct are listed, together with the typical posture and facial expression of the vocalising animal together with the situational factors, the response of other individuals, an alphabetic transcription of the call and an estimate of the duration where this was obtained. The list is in order of increasing intensity.

1. Soft arrr

   This call is given by all age and sex classes as far as could be determined, although it is not certain that it was made by infant ones. The posture of the animal making the vocalisation did not alter when the sound was produced, it was in fact a sound made incidentally during other activities such as feeding. The facial expression was the normal relaxed position

Fig. 27

Fear and aggressive components of agonistic vocalisations.



with no apparent muscular contraction, the sound was not directed at any particular stimulus, although the situation in which it was given was generally such as would indicate some degree of pleasure, such as feeding or being groomed. The response of other animals was either to reply with a similar vocalisation, or to make no response. This call occasionally intergraded with No. 2.

2. Soft grunt

This call was louder and longer than the soft arrr. Given by all age and sex classes, in no particular posture, and without apparent reference to specific factors in the environment. However, this sound was heard most frequently immediately prior to, and during grass ranging expeditions, and it is possible that it acts as a mechanism for promoting group unity under these circumstances. The response of other animals was often to give the same call in reply. The approximate alphabetic transcription is grr.

3. Soft call (alarm) (sac)

This call is given by all age and sex classes older than infant ones. The posture in which it is given is that in which the clearest view of the potentially dangerous stimulus is obtained, and the call is given whilst looking intently at the object. It was impossible to determine the details of facial expression as this vocalisation was never seen at close quarters. The mouth, however, is slightly open and there is apparently little lip retraction. This call has great social significance. It was only heard given to the distant approach of African fishermen. It was also probably given to the approach of the observers in the beginning of the study, but being low-frequency would not have been heard. The call is a short sequence of low-frequency arrrs. It is fairly loud, but even at the highest intensity was not audible to the observer at more than 20 metres from the source. Alphabetically, the call can be described as grr -- grrr -- grr -- grr. The duration of each call is about .75 to 1 second, with a similar pause between the components, but this is sometimes shorter.

4. <u>Cough oo</u>

This call is given by all age and sex classes, but particularly by adult animals. It is generally given when an animal has been startled by, for example, a bird suddenly flying close. The posture in which it is given is generally indicative of the "fright" which the animal has received, and it may be crouched, as if to run or jump away. The call is given whilst looking towards the stimulus. The facial expression seems identical to the classical startle respone. The reaction of other members of the group is vatiable, but it is not a call with a great deal of social significance, and often other members of the group only look towards the calling animal without interrupting the behaviour in which they are engaged. Generally only a single call but occasionally two are made. Alphabetically it can be written as U -- U with the second syllable variably present. The duration of each U varies between about ½ and 3/4 second. Displacement scratching and nose rubbing is very commonly seen in the individual after this call has been given.

5. <u>hu - hu</u>

This is a rather uncommon call and was only heard being given by adult males. In function it seems to be intermediate between the soft grunt and the guttural grunt. It was made when the vocalising animal was galloping quite fast either towards a disturbance in the group, or towards another animal for some reason. The facial expression was difficult to determine, but was apparently relaxed, with the mouth slightly open. The only overt result of this call was for other animals also running in grass also to give the same call. The call was characteristically a repeated sequence of low intensity grunts. Alphabetically it can be written hu - hu - hu, the duration between syllables varying from about .25 seconds to two seconds.

6. <u>Call to infant</u>

This call is made only by adult females to infants. It is not common, and is given to squealing or shrieking infants who are in trouble away from the mother. The posture of the mother is typically agitated as if looking for the infant, it was usually given when standing bipedally on the hind legs and looking round. The lips are pursed and opened only a fraction. The eliciting stimulus was usually the infant distress call, which was apparently individually identifiable by the mothers. Other group members often paused in their activity and looked round. Once the call was given by a mother who had apparently lost her infant and which was not squealing. He came running up to her when she gave it. The sound is a musical trilling noise, tending to terminate with a slight squeak. It can be written as rrrrrl - rrrrrl. The duration of each trill may be as long as two to three seconds, and the period between successive calls may be extremely short, less than 1/4 second.

7. <u>Infant distress call</u>

This call was only given by infant ones away from their mothers. It was apparently identical to the adult female call to the infant, and also apparently indicated distress and was frequently given when looking round. The lips are nearly closed but are slightly protruded. The response to this call was generally for the mother to come to the rescue, but other females also tended to approach the calling infant. If help is delayed, or if the danger is extreme, the trill may terminate in a squeal rather than a squeak. Generally, however, this is not the case. The call may be written rrrrri - rrrrrri. Generally a sequence of four to five calls is given. The duration and other temporal characteristics were very similar to those of adult females.

8. Guttural grunts

This call is given by all age-sex groups above infant twos. The posture is generally threatening, and it may be made with the classical threat face. It is commonly heard either during, or associated with the territorial "jumping-round" display. They are generally given in threat situations, and indicate a high level of aggression and very low fear. They were only given to members of the same species, and not to human or other intruders. The call has a great deal of social significance, and stimulates other animals either to give the same call, or to squeal if they are being threatened; a group that is trespassing in another group's territory and hears this call responds by dashing back to their own territory. The call may be either a single guttural grunt, or more commonly a series of repeated calls. The sound is very like that of the start of a chimpanzee chorus, and in fact on occasions may reach a crescendo. The call may be written gru - gru - gru. Each syllable lasts about ½ second, but the intervals between syllables is variable, and, as has been stated, tends to get shorter in any given sequence.

9. Loud cluck

This call was curious, in that although loud, invariant and given in similar positions, did not seem to refer to any particular aspect of the environment or social factors. It had no apparent social effects, although on one occasion was answered by a similar call. The call was given almost exclusively by adult females who were engaged in looking-out. The posture was typically alert, the caller often looking-out over the grassland, but never, as far as could be determined, at any potential danger. The mouth was generally pursed, the facial expression apparently relaxed. The call can be written krra - krra. It is a rather musical sound, varying in intensity and duration. Generally two or three calls were given at any particular time.

10. Chirrup

This call was given characteristically by juvenile males and adult females. It is a long-distance threat, being replaced as the intruder proceeds towards the group, by chittering. The posture is alert and threatening, but not a high intensity threat. The mouth is fairly widely open, but there is little retraction of the muscles around the lips. The response of other members of the group is to come and look at the disturbing stimulus, and if it appears disturbing to them, to also join in chirruping and chittering. It is a loud, mucial call, probably classifiable as a "cluck" in Andrew's scheme. It can be written chip - chip. Syllable may be repeated in a rapid sequence, or only appear singly.

11. Aggressive trill

This call was characteristic of territorial disputes, especially in grassland after a grass fire when groups were feeding in these areas. It is associated with high levels of aggression and is given with lips pushed forward, mouth only slightly open, frontalis muscle contracted, raising the eyebrows, exposing the white eyelids and widening the eyes. It is directed at animals of the opposing group. It may be made standing bipedally looking at the offending stimulus. It is frequently given by several members of a group simultaneously, and is often answered by members of the offending group also giving the same vocalisation. It often accompanies chasing, and the general impression of the emotional state of animals is of considerable agitation. A low-intensity version of this call was occasionally given to the observer. The call is a musical trill, similar in sound to the infant distress call, but often ending on a higher note than the one on which it started. The alphabetic approximation is krrrrrri - krrrrrri. The trill component is however variable in duration, lasting between about $\frac{1}{2}$ second and 1 second.

12. <u>Chitter</u>

This call is given principally by adult females and juvenile animals. It is an aggressive call but with a certain amount of fear. It is given in an alert position and directed towards the evoking stimulus. The mouth is quite widely opened and there is a variable amount of lip retraction. The situation is intrusion or annoyance either by other members of the population, or by other species. The reaction of other group members is similar to their reaction to chirrups; to come and assess the evoking stimulus. The call is staccate and classifiable under Andrew's scheme as a "sharp call", phonetically it approximates to ek - ek - ek. The syllable is made generally with expiration, but at higher intensities a short sequence with syllables on both inspiration and expiration may be made. This sounds like EKekEKekEK. The duration of each syllable is short, but the continuous sequence of inspirations and expirations may last 3 or 4 seconds. This call is often given repeatedly for an hour or more by a given individual if the evoking stimulus remains in the neighbourhood and visible to the animals.

13. Honk

This call is given by adult males only, and is presumably homologous to the chitter, but has a higher threshold. In all other respects is the same, and it may also be given in inspiration-expiration sequences lasting three or four seconds. This call is generally given later than the chitter, and stops sooner, not persisting in the same way as the chitter. It is a harsher noise than the chitter, and can be written ak - ak - ak, and the high intensity inspiration-expiration sequence, AKakAKakAK. This last noise is not dissimilar to the "gobble" vocalisation of male turkeys, although harsher in quality.

14. Squeal

The squeal is invariably associated with fear, but there is a variable aggression component. In a squeal that has very little aggression, the posture is cowed and cringing, the lips are retracted strongly showing teeth and gums; where there is aggression the posture is less cowed, although there is a tendency to crouch, and the lips are not as strongly retracted. The pure fear squeal was rare, and was given by an adult male that had trespassed into another group's territory and was caught by the adult male of that group. The response of other animals to this call, in the case of the fear squeal is to take very little notice, perhaps looking round; the aggressive squeal, on the other hand occasionally resulted in an animal dashing up and helping a female to chase a male, also by squealing in the same position.

There is a call which was never heard on Lolui, but which was heard in captivity, and when trapping attempts were made, which appeared to be intermediate between the aggressive inspiration-expiration sequence of honks, and the fear squeal. The sound was not unlike the geckering of rhesus, but more intense. There is no approximate alphabetic transcription of the squeal.

Postures with social significance

The distinction between movements and postures which have social significance and those which do not is always clear. The posture of standing on the hind legs and looking round in the grassland for example, only has social significance for those animals already in the grassland, or those about to embark on a grass-ranging expedition. An animal feeding in a vegetation thicket although perceiving the posture of the animal in the grassland, will not react to it. At the extremes, however, the distinction is fairly clear and it is possible to state that certain movements and postures have very little, if any social significance, and others always have some social effects.

The nomenclature to be followed in this analysis, as far as possible, will be that used by Hinde and Rowell (1962) in their description of the postures and gestures of the captive rhesus monkey, *Macaca mulatta*. In their introduction to this paper, the authors stated that as there was a certain amount of variability in the pattern of the postures they described, only the basic or fundamental type would be described. The same situation was also found on Lolui Island. It was interesting to note, however, that although the pattern of, for example, relaxed sitting, was very variable, certain typical postures served as quite reliable indicators of individual identification. An adult female of Group 1, for example, when having her perineum groomed, habitually adopted a posture in which the arms, from the elbow joint, were flat on the ground, with the head between them, whereas the hind legs were fully extended, with the tail curved forward over the back. Although this posture was occasionally seen in other animals, it was highly characteristic of her, and was adopted irrespective of the age-sex status of the individual which was grooming her.

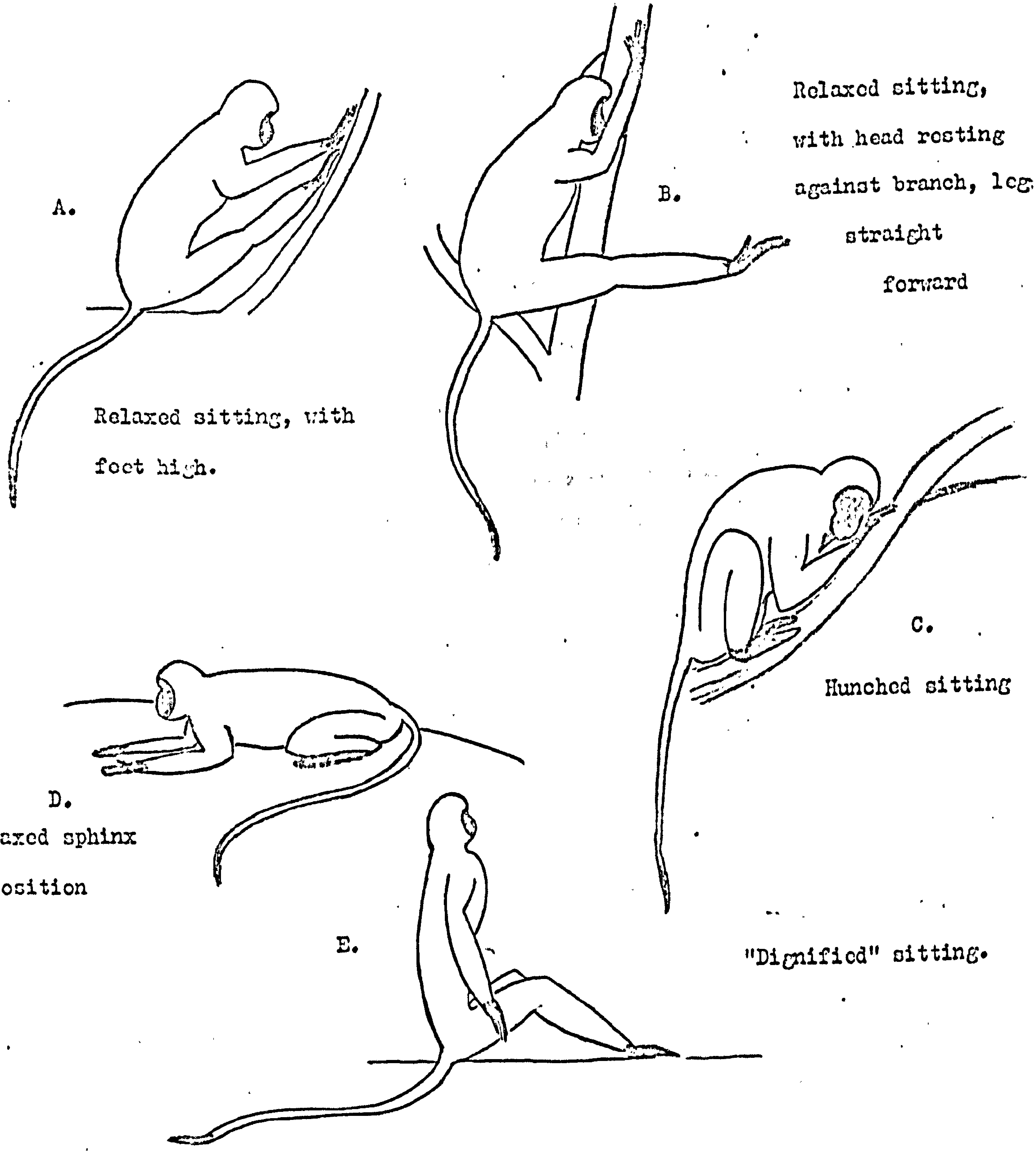
Sitting postures

The posture of a resting or sitting animal tells a great deal about the motivational state of that individual, and also about the physical condition of the animal; the two factors being often closely related. Thus it is generally possible to tell whether an animal is completely relaxed, alert, frustrated or "miserable", and, whether it is ill, or whether it has an infant. It was not possible, however, to correlate sitting posture with social status in the way in which Hinde and Rowell suggested. Thus, hunched sitting, which Hinde and Rowell considered to be the usual resting position of "middle-rank" monkeys did occur on Lolui (Fig. 28C), but had nothing to do with social status, and was observed only during heavy rainstorms and, in captivity, in animals that were unwell. It is possible that this posture in captivity is exactly the same as that observed under wild conditions, the approximate motivational state being "thoroughly miserable". Under captive conditions, therefore, the posture may only indirectly be a result of "social rank" and be directly the expression of discomfort arising from persecution, lack of space, or from any one of the many restricting factors functional in captive conditions.

1. Relaxed sitting.

Relaxed sitting on Lolui was extremely variable, and the

Fig. 28



A. Relaxed sitting, with foot high.

B. Relaxed sitting, with head resting against branch, leg straight forward

C. Hunched sitting

D. Relaxed sphinx position

E. "Dignified" sitting.

posture was adapted to the particular part of the environment in which the animal was sitting. Thus, if there was a convenient branch, the feet might be stretched straight up, resting on a branch, level with the head of the individual, or above it. (Fig. 28A). Or the head might be rested against a trunk or branch, with the hands holding on above the head of the individual, the feet either holding onto a convenient branch, or alternatively, with the legs stretched straight out (Fig. 28B). The common relaxed sitting posture on the ground is shown in Fig. 25A, but the positions of arms and legs relative to each other is very variable. A common relaxed position often observed on rocks, or other flat, hard surfaces is that shown in Fig. 28D. This was called the relaxed sphinx position and was commonly observed in animals which were being groomed, as well as in resting animals. The factor which all these postures have in common, except for the sphinx position, is a fairly gentle curvature of the spine, with the point of maximum curvature slightly anterior to the middle of the back, although even this was potentially modifiable if the position of the sitting place so necessitated.

2. Hunched sitting

Hunched sitting was, as has been noted, associated with heavy rain rather than social position. In captivity it was also commonly adopted by animals which were ill.

3. Upright sitting

Upright sitting (Fig. 28E) or the "dignified" sitting position was a posture that was associated with social factors. It was commonly seen in animals that had been chased, especially adult males who had been chased by females. Although similar to the sit-threat, it was not directed at the chaser, and in fact the posture did not generally appear until the chasing animal had moved away from the scene. However, the posture then was often maintained for thirty minutes, and occasionally longer. The animal would move, not necessarily remaining in the same area in which the chase occurred, but after walking, would re-adopt this posture.

4. Crouching

Crouching was generally observed during aggression, in the animal which was the victim of the aggression, and also, but more variably, in the aggressor. Crouching was also commonly observed in animals approaching another which they had reason to suspect might attack them. It was a component of female presenting. In any approach of one animal by another in which the approaching animal had some slight motive for fear, then crouching was observed.

5. Protective sitting

Protective, or maternal sitting (Plate 29) was a very characteristic posture of adult females with infant ones. It was in fact a very accurate diagnosis of the presence or absence of infants, a point which was not always evident at first sight. This posture had nothing to do with the social status of the mother, but was adopted by all adult females with infants, from the very first. Part of the reason for this position is no doubt purely mechanical, the weight of the infant causing the modification of the normal sitting position, but this cannot be the entire explanation, as the older and heavier the infant becomes, the less pronounced becomes the protective position. The posture can be seen to be a modification of the relaxed sitting posture, with more pronounced curvature of the spine, and the point of maximum curvature being slightly more anterior than is common in relaxed sitting.

Other postures recorded by Hinde and Rowell in rhesus were observed on Lolui, but again had apparently more to do with climatic factors and little with social. For example, cat-like sitting was occasionally observed, but this was common

Plate 29. Adult female with infant one. The posture is the typical maternal protective sitting position. Note the strong curvature of the back.

on cool or relatively cold mornings, when animals were sitting on dew or rain-soaked rocks in the undergrowth, before starting on the day range proper. It was a posture associated with a less intense level of discomfort than was the case with hunched sitting.

Sleeping in huddles, as recorded by Hinde and Rowell, and by Brain (Gartlan and Brain, in press) for *C. aethiops* was not observed on Lolui. Brain suggests that in South Africa it occurs during cool or cold weather. Temperatures of the extremes encountered in South Africa were not recorded in East Africa. It seems likely, therefore that this again, is a pattern dependent on climatic factors in this particular species.

Aggressive postures and threat.

Evidence on increased aggression in this species as a result of captive conditions was presented in the section on age and sex distribution. Under cage conditions an increase in the mean area per animal of from 123 cu. ft per individual to 267 cu. ft was reflected in a decrease in aggressive incidents from one per 12.4 minutes in the smaller cage; to 1 per 28.6 minutes in the larger one. It is not surprising therefore to find that aggressive behaviour does not play as large a role in the behaviour of the species under natural conditions as would, perhaps, be expected from captive data. Further evidence to support this point of view will be presented in the section on the patterns of social organisation. Here it will be sufficient to note that in general there is less than one aggressive incident per hour.

The main threat postures observed in reaction to the human observer have already been described, (Fig. 26), and the extent to which these were observed in inter-animal interactions has also already been indicated. In general, however, it was apparent that an animal that was likely to be attacked could prevent this by not subjecting itself to the possibility, by avoiding potential aggressors. This is not always possible in cage and compound situations. Thus the posture described by Hinde and Rowell as the attacking run was observed on Lolui only rarely, although common when a human observer attempted to enter a cage in which the captive vervet group lived.

1. Attacking run and bounce.

The complete sequence of this posture and behaviour was only ever seen in adult males, although females occasionally carried out incomplete parts. The attacking run almost invariably commenced with a threat-face, with the animal in crouched position. The frontalis muscle was strongly retracted, with the eyebrows drawn back, and the eyes very wide. The lips were closed and thrust slightly forward. The ears were generally retracted, and the body fur was occasionally raised. The tail was generally held vertical, but this was variable. The posture was generally assumed only three or four feet from the object of attack, and runs were short, and each step tended to be made in a crouch, ending with a short bounce, hind legs on the ground, forelegs off the ground. High intensity guttural grunts were occasionally made. No animal was ever seen being bitten or attacked as a result of this posture, which in spite of its rather spectacular nature, seemed to embody a certain amount of fear. The only times that animals were seized and bitten (and this was observed only twice in serious aggression, as distinct from play or other social biting), the attack was swift and silent with none of the bouncing and apparently no threat facing, although this was impossible to tell clearly from the two incidents that were observed. In general, threats seem to be ritualised and attack inhibited. This is almost certainly not the case in other populations of the same species.

2. Bouncing

The role of bouncing in threat has already been described. In general it seems to indicate ambivalence between threat and fear. Hinde and Rowell suggested that in rhesus it was essentially the same as branch-shaking, modified because of the stable surface on which it took place. In C.aethiops bouncing seems to be a distinct behaviour pattern, and branch shaking in the sense used by Hinde and Rowell, does not occur, although a spectacular shaking of branches is observed in the territorial display "jumping round". The shaking here is by the whole animal jumping from branch to branch of the high canopy and not holding onto a single branch and shaking it in the manner described for rhesus.

3. Striking

The striking of another animal with the hand is a very rare aggressive pattern. It was observed only on three occasions; once an adult male eating a püffball was approached by an infant two, who showed a great deal of interest in the remains of the fungus which were still in the ground. It started to scrape at the soil, about 18 inches away from the adult male, slightly to the front of the male and on his right. The male struck the infant by bringing the arm in a single smooth arc, with fingers together and palm forward, hitting the infant near the middle of the back. The infant sensed the beginning of the blow and jumped, but not soon enough to avoid being hit, and was knocked several feet by the force of the blow, but was not injured in any way. The other two incidents were of adult females also hitting infant twos.

4. Tail erection

Tail erection in the adult male vervet gives a conspicuous display of the red anal area, the white fur between anus and scrotum and the bright blue scrotum. It is seen most commonly in territorial disputes and seems to act as a focus for the attention of other members of the group. It is very common in a territorial dispute in grassland to see the two opposing males facing each other, several yards apart, with tails vertical, and each attended by several adult females, who alternate between a rather frantic grooming of the male, and high-intensity aggressive-trills. Tail erection on Lolui was only associated with agonistic postures and seemed always to act as a focus for other members of the group. Normal walking through the grass was usually with the tail held horizontal and curving down for the last six inches or so. This was not the case with Starck and Frick's populations (1958), nor with the population studied by the author at Chobi, where every individual starting to move through the grass walked the first few ywards with tail erect. Thus, an animal gradually moving through the grassland, sitting and then walking a few yards, gave continuous signals of his position which were of particular value under the conditions of Chobi, which were rather impoverished and meant that groups foraging in the grassland there were always much more dispersed than was the case with the Lolui population.

Very occasionally tail-lashing, in a very similar manner to that observed in cats was observed in adult male vervets on Lolui, and seemed to precede threats. It was only observed five times.

The facial expression and posture of an animal is used by other animals as an index of probability of attack. If, for example, an animal is sitting sunning itself on a rock, and another animal also approaches the same rock, the approaching animal often gives a quick glance at the face of the animal already there before moving to join it. This is a very common behaviour pattern in all age and sex classes; an animal can be seen walking unconcernedly through the grass, feeding as it goes, passing other animals which may be sitting or resting each one of which is given a quick glance. This is one way in which aggressive incidents are minimised. Most of the time an animal surrounded by others has at least some knowledge of the motivational state of those around him. If an animal is aggressive, it generally happens that others keep out of the way. Most social aggression occurred when this continuous monitoring system broke down. An animal slipping off a branch, for example, and falling onto a rock where another animal, or pair of animals would be sitting grooming, would be usually chased off by both. Social monitoring of this type can be seen to increase greatly under captive conditions, and the captive vervet group was conspicuous in the high frequency of this type of behaviour. Hardly any movement, and certainly no feeding was undertaken without looking round at the position and disposition of the other members of the group. The behaviour is difficult to quantify as it is so rapid and cryptic. An animal can glance at another without moving its head. However, a short study was carried out on the captive group at Bristol, the criterion being a glance involving a clear head movement, The constitution of the group was abnormal, being 2 AM, 4 AF and one JM. Observations of one hour each for a period of ten days were carried out. No less than 1104 incidents were observed, of which 420 were by the juvenile male, 584 by the adult females and 100 by the adult males. This gives a mean number of monitoring incidents, per hour for the group of 110.4, which is certainly a great deal higher than the normal rate observed in the field, although no quantitative data was obtained to support this contention. The same age-sex pattern was also thought to hold true for the field study, namely that most of the monitoring was done by juvenile animals taking note of adult animals, rather than their peers.

Fear

Some of the considerations which applied to aggression and captivity also apply to fear postures. The posture of looking elsewhere, for example, which was recorded by Hinde and Rowell, was not observed as part of the normal behaviour repertoire of C.aethiops in the wild, although it occurred in captivity. There is no need for this "cut-off" posture. If an object is alarming, the animal has the whole territory and can move elsewhere. Captivity, as it increases the incidence of aggression, might also be expected to increase the frequency and intensity of fear behaviour.

1. Frightened grin

The frightened grin, described by Hinde and Rowell appears to be exactly similar to the facial expression adopted by C.aethiops in similar conditions. It was always present when the "fear-squeal" vocalisation was given, and in fact it was the lip retraction which gave the vocalisation its distinctive sound, permitting field recognition by sound alone, in the absence of visual evidence. The expression was rather rare in the field, but was much more common in the captive group.

2. Locomotion and fear

Locomotory postures are good indicators of fear, and much more common than the rather extreme fear grin, mainly because animals who are frightened remove themselves from the presence of the frightening object. The normal galloping locomotion of animals running in grassland has already been described. When the animals were frightened, the stride was much lengthened, and the bouncing aspect of this locomotory pattern disappeared entirely, the animal being generally stretched out and close to the ground.

An animal that has cause to fear another animal often moves out of the way with a very characteristic posture, slightly crouched, the tail depressed, and the legs moving quite fast. Often this locomotory posture is accompanied by rapid glances round at the animal from which the movement is made.

Crouching is an almost invariable accompaniment of fear. In general it may be stated that the higher the level of fear, the more pronounced is the crouch. At very low levels of fear, or apprehension, in grassland, however the bipedal stance is often adopted.

Friendly behaviour

Patterns of grooming, lipsmacking and sexual behaviour will all be dealt with at length in separate sections. In the meantime, it is only proposed to state that all these behaviour patterns are taken as evidence of positive or attractive valencies between different members of the group. Maternal behaviour, although different in aetiology and function will also be considered under this heading, as it also is indicative of positive social vectors, which tend to promote group unity.

Olfactory communication

The sense of smell is very important in the everyday life of the vervet monkey. The suitability of many items of diet are assessed by this means, and many social patterns involve sniffing either another individual or the place where another individual has been.

The ano-genital region is very often sniffed by other animals. This begins in infancy; the newborn infant is subjected to prolonged visual and olfactory investigation of the ano-genital region. Whether this has any role in the release of urine and faeces by the infant is not definitely known, but it seems possible that it does. It certainly had this role in a captive group of the closely-related Erythrocebus patas.

As the infant gets older and begins to make expeditions away from the mother, the first reaction on the part of the mother on finding the infant after losing contact with him is to give it a swift sniff, or nuzzle in the centre of the back. The precise function of this behaviour pattern was not clear, as no mother ever rejected an infant on the basis of this inspection. A very similar behaviour was also observed in copulation, the mounted male either sniffing or nuzzling the back of the female immediately prior to beginning pelvic thrusts.

The place where an animal has urinated is often sniffed by other animals coming to the spot. Infants often sniff the fur of other animals. Twice an adult female was observed to sniff pungent, decaying matter on the ground and then to roll on it, in exactly the same manner as observed in dogs, several rolls followed by another sniff, and then several more rolls again. The role of olfaction is perhaps most important in territorial marking which is performed by members of the Lolui population, and which is in part a scent marking. The details will be presented in a separate section. Here it will just be stated that the marking is either by rubbing the chest against a branch or rock, or by rubbing the angle of the jaw against branches. The latter pattern has since been confirmed from captive studies both in this country, and independently in South Africa (M. Lyall-Watson, pers. comm.)

Sexual behaviour

The sexual cycle

Cercopithecus aethiops, like all other members of the genus (the Talapoins being considered as belonging to the genus Miopithecus) lacks the sexual skin which surrounds the ano-genital area of female baboons and chimpanzees, the state of turgesence of which provides external information about the state of the reproductive cycle. It is, accordingly, rather difficult to ascertain from external observation the state of the cycle in this species. The problem is made more difficult by the absence of external evidence of the menstrual flow, which can only often be detected by means of vaginal lavage. In the field menstural flow was only ever observed in pubescent females, which occasionally showed also a slight turgesence of the ano-genital area, with a reddening of the skin. But these were variable and did not provide sufficient reliable evidence on which to draw conclusions about the duration of the menstrual cycle.

Zuckerman (1935) observed menstruation in a group of 12 captive C.a.sabaeus only once in each of three animals. In another female, four successive cycles were recorded at intervals of 16, 32, 52 and 32 days. The same author (Zuckerman, 1938) recorded a specimen of C.a.aethiops which menstruated regularly at intervals of 31 days, the flow lasting for about 2 days. These data, derived from captive studies underline the difficulty in obtaining reliable data on this aspect of reproductive physiology from field observation alone. However, the data on baboon and macaque matings show that there is a tendency for copulation to occur most frequently at about the times of ovulation, decreasing in frequency during the luteal phase, and ceasing during menstruation. This at least provides a means of establishing the presence or absence of periods of receptivity during the menstrual cycle, and the durationof such periods, so providing indirect evidence of the duration of the cycle. The observed copulations of identified females in Group 1, together with those females observed with semen on the vulva are shown in Table 19.

TABLE 19

Observed copulation by identified females of Group 1, and females observed with semen on the vulva.

Date	Individual	Frequency
10.10.63	JF2	1
13.10.63	JF4	1
16.10.63	JF2	1
18.10.63	AF2	1
21.10.63	JF2	1
22.10.63	JF2	2
23.10.63	JF5	semen
	JF1	semen
8.1.64	JF5	1
	JF2	1
10.1.64	JF1	1
	AF4	1
11.1.64	JF2	1
16.1.64	JF1	1
27.2.64	AF4	1
29.2.64	AF4	1
3.3.64	AF4	1
6.3.64	AF4	1
19.5.64	AF1	1

It is impossible to draw definite conclusions from the above data, but it is possible to state that the observations on JF2 are compatible with a menstrual cycle of 30-31 days, with an observed receptivity period of 13 days within the cycle. The receptivity period indicates the magnitude of possible error on calculations based on single incidents only. JF1, on data that is possibly unreliable for the previously mentioned reason, showed a cycle compatible with a mean duration of 26.6 days, with an observed receptivity of 7 days. For AF4 the cyle fitted a periodicity of 25 days, with an observed receptivity of 9 days. In general, therefore it may be stated that the Lolui observations are not incompatible with Zuckerman's data in this respect.

Sade (1964) has observed seasonal variations in the size of the testes in a captive population of Macaca mulatta on Cayo Santiago and Sade and Hildreth (1965) have recorded seasonal variations in testis size of C.a.sabaeus on St. Kitts. No detailed investigation of this possibility was carried out on Lolui; the population was interfered with as little as possible. The penis was completely retractible in this species, and the testes were occasionally retracted, but this was not a seasonal phenomenon, and also had apparently nothing to do with social factors. The reason for the retraction was obscure; in general it only lasted for less then five minutes. It was only observed on four occasions. In the section on birth periodicity, it was noted that there is a distinct copulation season. The physiological basis for this is not known, nor is it known whether there are differences in the menstrual cycle of females at different times of the year, nor whether males also show seasonal variations in ability to copulate.

Initiation of copulation

Copulation may be initiated either by males or by females. In those incidents in which it was clear whether one partner initiated copulation, 14 approaches were by adult males, and 15 by adult females. In addition to these, which all resulted in copulation, eleven approaches by males were refused by the females, and seven by females to males were refused, with an additional two in which grooming rather than copulation resulted.

There is no apparent "invitation" posture on behalf of males prior to copulating. They approach the female, who either takes no notice, or adopts a receptive crouch, runs away, or threatens the male and chases him. A willing female is one who stays in the same place when the male approaches her. If the male has approached from the front, he moves round to the rear end of the female, and mounts without prior ceremony, although occasionally sniffing the perineal region.

Initiation of copulation by females is much more clear cut. The female generally follows the male, then at some point stands quadrupedally in front of him, slightly crouched, the tail moved slightly aside from the perineum, and either glances over her shoulder at the male, and back again, or looks fairly fixedly at him. No vocalisation or change in facial expression was observed. The extent of the crouch, and of the tail moving was variable. This "presenting" was only ever observed in the sexual context and had not become ritualised into a social gesture as in baboons, nor was it ever, therefore, ever seen performed by male animals.

In mounting, the male held onto the ankles of the slightly crouched female with the feet, the thumbs were opposed, and the toes also clasping the leg. The hands held onto the fur of the back just anterior to the groin. The first behaviour after this was invariably for the male to bend down and sniff or nuzzle the back of the female with a single swift movement. It was not a bite. Then he assumed the almost upright posture and began the pelvic thrusts. The number of thrusts was variable, the mean number being 9.5, and the range from 3 to 15. The thrusting rate varied between 1 and 1.5 per second. No vocalisation was ever observed during copulation and apparently little alteration in facial expression, although some evidence of lip retraction in both males and females was observed.

Between the onset of the pelvic thrusts and prior to the ejaculatory pause, a thick white paste-like substance was observed being extruded from the vagina. It seems likely that this was from the male. It was not semen, and occurred apparently prior to ejaculation, as thrusting continued after and during the time that it was extruded. The possible nature and function, if any of this secretion are not understood. After ejaculation there was an ejaculatory pause, when the penis remained in the vagina for between 3 and 5 seconds before being withdrawn. This was used as an index of complete copulation.

After the withdrawl of the penis, the female invariably ran forward away from the male at least three feet, although on one occasion an immediate and intense grooming session started before the female had chance to run away. She was restrained by the male. The postcopulatory run was in a crouched position, very similar to the posture adopted by the female in copulation. Often the female returned to the male after sitting apart from him for up to four minutes, and grooming then resumed.

Homosexual and inverted mountings were occasionally observed. No male was ever observed to mount another male, but there were five incidents in Group 1 of an adult female mounting another female. These incidents were all by females which were apparently sexually receptive and which had been or shortly were to be, involved in normal copulation. Mountings of a male by a female were seen on two occasions, in both cases the females had been presenting to the males who had taken little notice.

No masturbation by males was ever observed, although spontaneous penile erections were common. Handling of the erect penis was rare, and observed in adult males only on ten occasions in Group 1. Generally the handling was for the purpose of removing a foreign body from the penis.

The ano-genital areas were particular areas of social interest and were one of the main areas of grooming. The reasons for this interest are probably manifold, but were almost certainly not exclusively sexual. Faecal remains were often removed in such grooming bouts, as were foreign bodies picked up in this area whilst sitting down. The anal area of males was also similarly treated, but rather less attention was paid to the penis and scrotum.

Erections are observed in infant twos, and juvenile males are capable of penetration and copulation, but in fact they rarely take the sequence as far as the ejaculatory pause. Mounting, apparently by infants of both sexes; appears very early in the behaviour repertoire and is commonly observed in the fourth month of life.

Copulation is apparently not inhibited by social factors due to the presence of other animals, and in this respect the population is different from many baboons (Zuckerman, 1932; DeVore, 1965; Hall 1962 ;) and macaques (Altmann, 1962). The only sense in which the presence of another animal inhibits copulation is if an animal is apparently accidentally disturbed by another during copulation, in which case the attempt may be broken off. No incidence of aggression against an animal as a direct result of copulation was ever observed either on the

the part of males or females.

Copulation did not take the form of a copulation series, as has been described for macaques (Carpenter 1942, Altmann, 1962) or baboons (Hall 1962). Each copulation is a discrete event, and which is apparently followed by a lengthy latency period. Only once was an identified female (JF2) observed copulating twice in one day, and these two events were more than ten hours apart. The refractory period for males was apparently shorter, and AM5 was once observed copulating twice within two hours, with different females.

Friendly behaviour

Self-grooming (Plate 30) is a behaviour pattern that is observed throughout the day, and may appear whenever an animal is resting, and it usually takes place in a modified relaxed sitting position. However, self-grooming is generally only a grooming of accessible parts of the limbs, arms legs and tail. The perineal region, the back and the neck and face which are those areas commonly groomed in mutual grooming are very rarely involved in self-grooming. Indeed, it is physically almost impossible. Social grooming, therefore, apart from promoting positive social bonds between individuals of the group, also is individually important in that generally those areas are groomed which are inaccessible to the individual. For this reason, solitary males which were observed, frequently had a "scruffy" and rather unkempt appearance, this was true of AM5 when he joined Group 1, his fur having a matted appearance, especially on the back. This did not disappear entirely for

for several weeks.

Initiation of social grooming, like copulation, may be either by males or females. The essential characteristic of the behaviour was that it was mutual with a frequent reversal of roles. This was true of all dyads, but in male-female grooming the convention of role reversal was very little more than a convention. After a lengthy period of the female grooming the male, she would sit to be groomed and sometimes would only be rewarded by a few seconds of perfunctory grooming with one hand.

The main postures used for soliciting grooming are short-range visual ones, and are generally performed within two feet of the intended partner. Occasionally longer-distance intention is signalled by lipsmacking. The animal approaching the putative partner often in this case does so with the face slightly up-tilted. The intensity of the lipsmacking varies from extremely violent, the noise of the smacks being audible several yards away, to an extremely slight and cryptic movement.

The two main grooming soliciting postures are, first to sit in front of the potential groomer in a relaxed position , but with the back rather straighter than in the relaxed sitting position, with the chin up in the air, exposing the throat. This is the commonest grooming invitation posture. Secondly, and very common in adult female dyads, and by adult males when inviting females to groom them, is for the soliciting animal to lie in front of the potential groomer, sometimes so close as to be actually

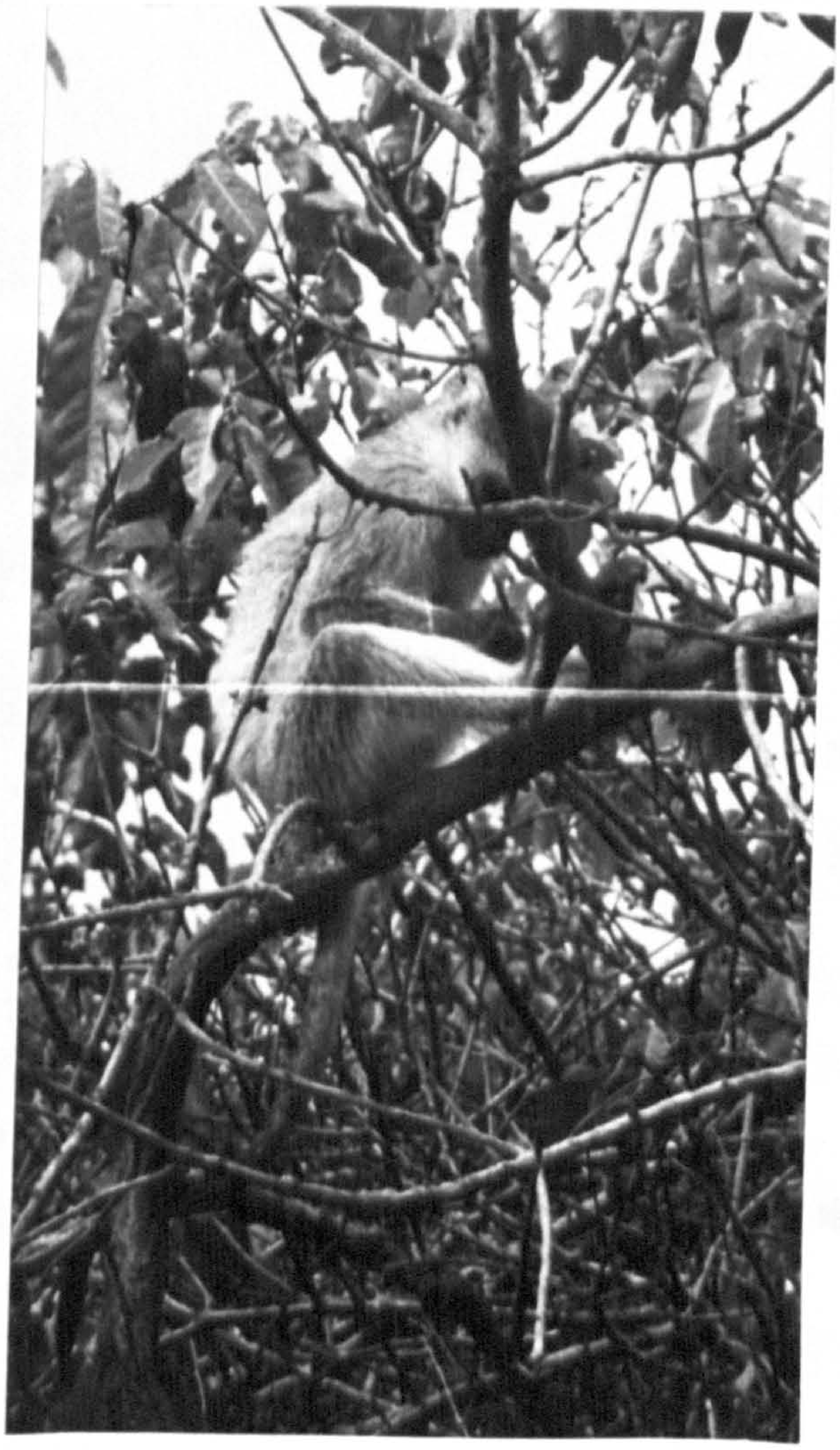


Plate 30. Subadult female engaged in self-grooming. Note the relaxed position and the fact that it is the limbs that are being groomed; in fact in this case the back of the left wrist with the fingers of the right hand.

resting on the feet of the individual in question. A less common invitation was to present the perineum. This was only observed as an invitation posture in adult female dyads, although it occurred as a grooming posture in all age and sex classes. The reason for this difference is not clear. This posture was different from the sexual presentation. The presenter stood with the ano-genital close to the intended groomer, with the tail either vertical, or curving over the back, exposing the entire ano-genital area to the groomer. No glancing or looking back at the potential groomer was ever observed in soliciting for grooming, unlike sexual presentation, and no crouching was observed; the soliciting animal standing quadrupedal and foursquare.

Postures adopted during grooming were variable, but were mainly characterised by being extremely relaxed. This was particularly true of animals lying on their side to be groomed, which often had arms and legs hanging loose and eyes closed. The main postures adopted are the following.

1. Sitting with throat up.

This posture (c.f. Plate 31) is characterised by the relaxed sitting position of the animal being groomed. The chin is held up, and the head moved from side to side whilst the fur around the neck and the front of the chest is groomed.

2. Sitting with arms upstretched.

This posture is commonly adopted when the upper chest

Plate 31. Adult female grooming adult male. The male is sitting in the relaxed sitting posture, with head up and face turned to the right so that the fur of the left of the neck can be groomed.

Plate 32. Adult female closely grooming the fur of the upper part of the chest of an adult male who is lying with arms stretched out.

and area under the arms is being groomed. The arms are also often stretched out in this manner when the animal is lying on its side being groomed.

3. Lying on the side.

This posture is usually completely relaxed. The area groomed is controlled both by the groomer and by the groomer, who moves parts of the body to be groomed close to the groomer. Plate 32 shows the same grooming bout as Plate 31, but the male is now lying on the rock with his arms stretched out whilst the female closely grooms the fur of his upper chest.

4. Sphinx position.

This position (Fig. 28D) is a common resting posture, and is also observed during grooming. It usually occurs at the beginning of grooming bouts, and is used for grooming the back and the head.

5. Rump in air.

This is a modification of the sphinx position, and is used in grooming the perineum. The chest is close to the ground, with the arms forward as in the sphinx position, but the hind legs are extended, with the weight taken on the feet. The tail is curved forward over the back. This was occasionally observed in most adult females, but was a characteristic posture of AF2 in Group 1, who adopted it much more frequently than any other animal.

6. Tail up or aside.

The tail is often moved aside from the ano-genital area for grooming, either being put vertical, or curved forward over the back.

The mechanics of grooming.

Grooming is characteristically a careful and rather intense activity. Animals can often be approached more closely before becoming aware of danger when they are absorbed in grooming. The hand movements are rapid, and hands are frequently alternated. The main positions used are the following.

1. Two handed grooming

In this method the fur is moved back, usually against the grain with one hand, whilst the searching and picking is done with the other. Occasionally both hands are used and the picking is done by means of the lips and tongue. Characteristically, the face is held very close to the part being groomed, and a sharp look-out for foreign bodies is maintained.

2. One-handed grooming

This is characteristic of self-grooming, or low-intensity mutual grooming, and often used by adult males to fulfill their "turn" in a mutual grooming episode. Often the index finger is extended, and this drawn through the fur, against the grain. Foreign bodies are picked out with the lips or teeth.

Foreign bodies located during grooming are removed either with the fingers, being firstly disloged with a scratching movement of the index finger nail, or with the lips and tongue. This perhaps explains lip-smacking as a ritualised grooming-intention movement. When a foreign body has been located, the fur is held back by both hands, and the face is brought close to the body, and then touched with the tongue, if this is sufficient to remove it, the object is taken into the mouth on the tongue. If the object cannot be removed by simply adhering to the tongue, then the lips and the teeth may be used. In very firmly embedded objects, such as the latex of Saba florida, the foreign object may be bitten out of the fur with the incisors.

These grooming mechanisms were confirmed by informal experiments on a semi-tame animal who both liked to groom and be groomed by human beings. Any blemish or flaw, such as a mole or a freckle would receive particular attention, and if the animal were not prevented, it would scratch the blemish with the index finger nail, and bite gently with the incisors until blood was drawn. This probably explains the need for some control over the part being groomed by the groomed animal itself.

Grooming, as distinct from being groomed, also seems to be a "pleasant" activity although was not as sought after as was being groomed. Occasionally a certain amount of force was used in pulling an animal down from a sitting position to a lying position for grooming. Force was also used in pulling the head of the animal being groomed down so that the top of the head could be reached. No animal was ever seen objecting to being manipulated in this manner. On two occasions juvenile animals standing quadrupedally were thrown to the ground by other juveniles for grooming. This was accomplished by the potential groomer putting its arms round the neck of the intended recipient and throwing it over onto its side, and then starting to groom. This is probably a relic of play-behaviour, as this throwing over is a common component of grapple-and-bite play.

Grooming is sometimes associated with sexual activity. Two incidents of sexual presentations by females being refused but turning into grooming bouts have been mentioned. Grooming was also seen after copulation, and frequently preceding mounting, even if full copulation was not achieved. Quantitative data will be given on the frequency of this sequence.

Quantitative data

The following information on the frequencies with which different age-sex classes groomed one another, the duration of bouts, etc., were all obtained from Group 1 during May 1964.

Initiation of grooming.

In social grooming dyads where the partners were of different sexes the initiation of grooming showed marked differences according to sex and age. In all dyads in which adult males and subadult and juvenile females were involved the initiation of grooming was by the male. The same was generally true of dyads involving adult males and adult females, but on one occasion the initiative was taken by the female. However, two incidents have already been described in which a female sexual presentation was refused by the male but which resulted in a social grooming episode. These incidents occurred outside the period illustrated in Fig. 29 and they are therefore not included in the analysis.

In dyads involving adult females and the juvenile male, seven in all, five incidents were initiated by the male and two by the females. Where subadults and juveniles were involved in opposite-sexed dyads, grooming was initiated twice by females and three times by males.

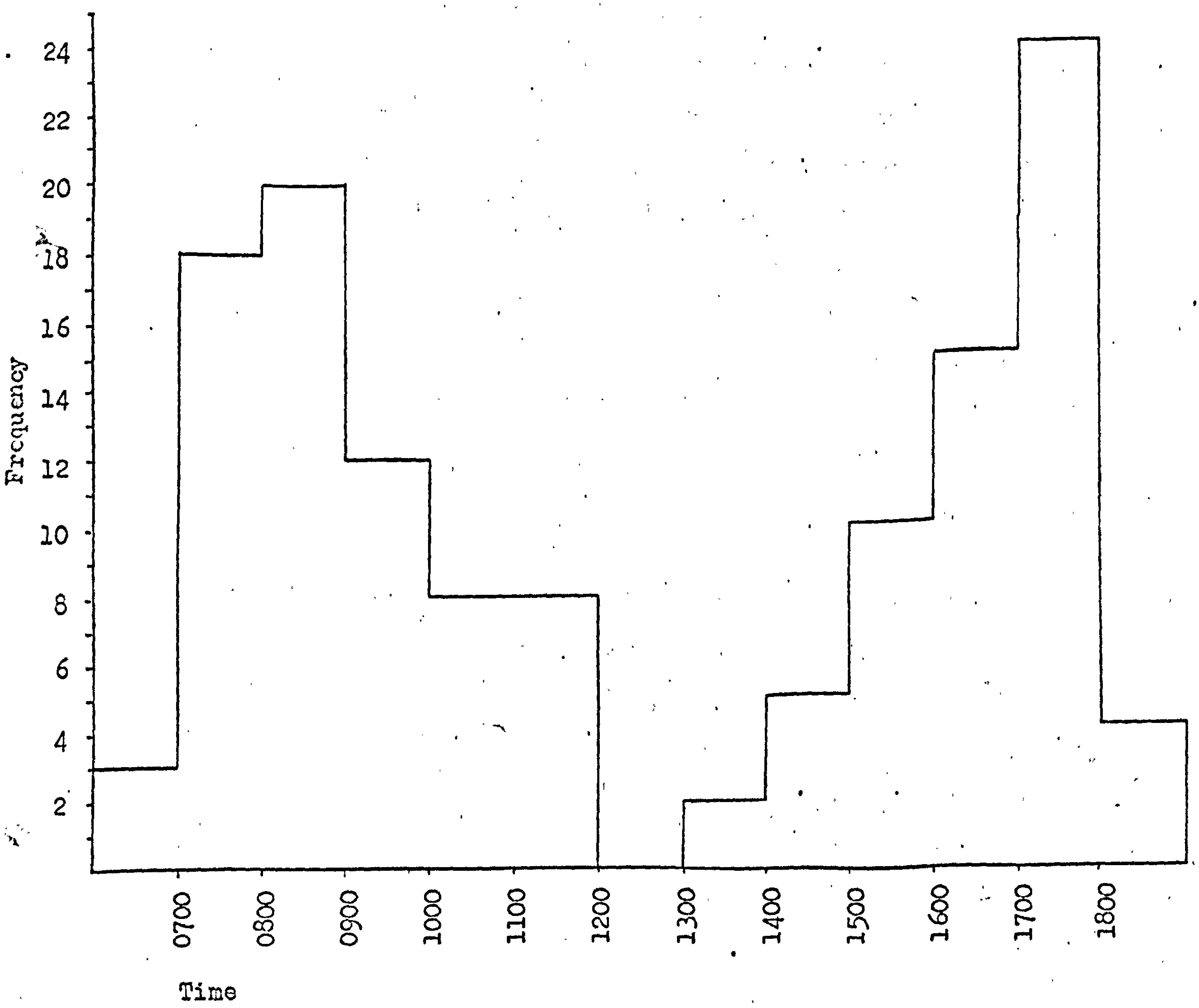
Like sexed dyads

No incident of male grooming male was ever observed. When adult females were involved with subadults and juveniles the initiative generally came from the older animal, this was observed in nineteen out of twenty-six instances. There was apparently no consistency in the initiation of grooming when adult females were involved with adult females. Thirty-two instances were observed but the initiation was only observed in nine cases. Of these, four involved AF1 and AF2, two were initiated by AF1 and two by AF2. AF2 also initiated grooming with AF5 on one occasion, and AF5 was also observed to initiate grooming with AF1 on one occasion. AF1 was observed to initiate grooming with AF3 on two occasions, but AF3 was not observed to initiate grooming with AF1. In like-sexed dyads involving juvenile and subadult females, initiation was only observed twice, and was by subadults.

In most social grooming bouts grooming by one animal is reciprocated by the other animal and the behaviour can properly

Fig. 29

Total frequency of social grooming in Group 1 between 7.5.64 and 26.5. 64.



be called mutual grooming. The main exception to this tendency was observed in those dyads in which adult males were involved. Of the 50 incidents involving adult males, in 29 cases the grooming was not reciprocated by the male. In several other cases the male reciprocated but only in a perfunctory manner, grooming the female with one hand at arm's length. In one recorded bout of 27 minutes duration the male groomed the adult female for only 47 seconds. Only 5 of the bouts involving adult females were not reciprocated (excluding the incidents in which the male failed to reciprocate). It rarely occurs that animals groom one another simultaneously. Throughout the entire study this was only observed on 8 occasions, and all of these involved adult and subadult females. The largest number of reciprocations observed was seven, but in the period illustrated in Fig. 29 it was four, this was an adult female-adult female dyad. (A detailed analysis of the data presented in Fig. 29 is presented in Table 20.)

Time and duration of grooming.

In general, social grooming occurs most frequently at the end of the day rather than at the beginning, although it is common at both times. Fig. 29 shows the time at which the 129 recorded bouts occurred between 7.5.64. and 26.5.64. It can be seen that social grooming increases up to 9 hr, after which it decreases until 13 hr, increasing then steadily to reach a peak between 17 and 18 hr. then decreasing rapidly

TABLE 20

Analysis by dyads of the data shown in Fig 29.

Dyad	Frequency	Dyad	Frequency
AM - AM	0	AF - JF	13
AM - AF	39	SF - SF	0
AM - SF	5	SF - JM	4
AM - JM	0	SF - JF	7
AM - JF	6	JM - JM	0
AF - AF	32	JM - JF	1
AF - SF	13	JF - JF	2
AF - JM	7	Total frequency	129

as dusk falls. In general, the peaks coincide with the time of day when grass ranging is commonest (c.f. Fig. 22) and in fact much social grooming takes place either on rocks or in termite mounds in the grassland.

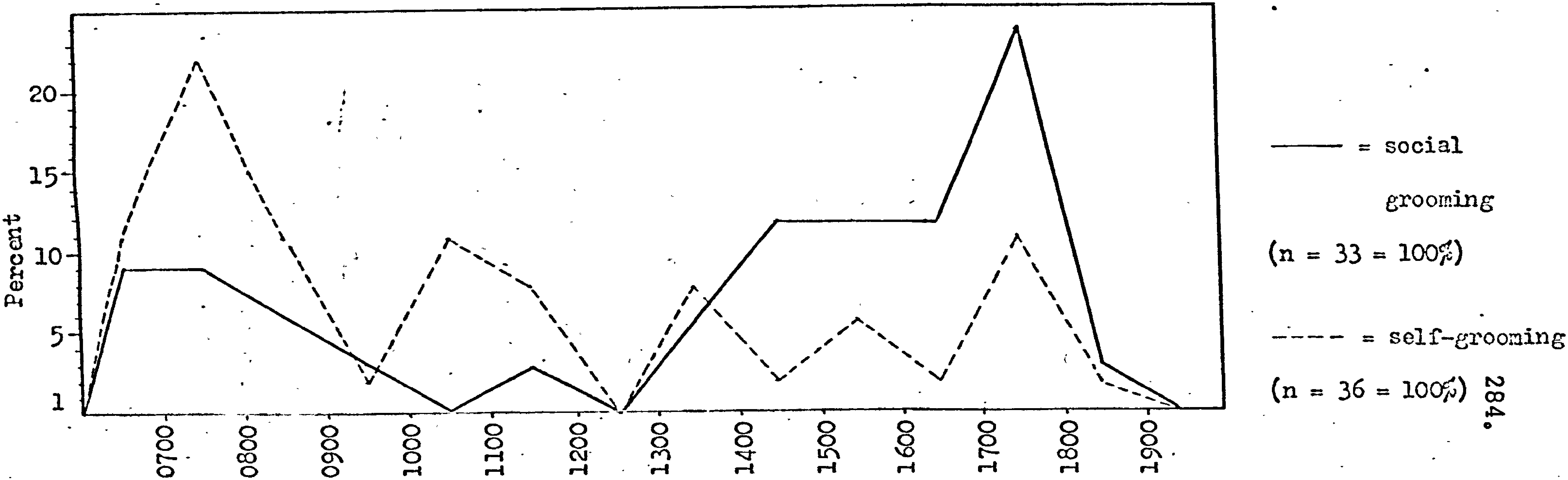
Fig. 30 shows a detailed analysis of the amount of social grooming compared to self-grooming for a five day period between 18.5.64. and 22.5.64. The pattern which emerges is fairly clear. Self-grooming reaches its highest peak fairly early in the morning, and generally before feeding has begun. Thereafter it decreases, showing lower peaks and troughs throughout the day and increasing to a secondary peak between 1700 and 1800 hrs. Social grooming, on the other hand, although increasing in the morning shows a much clearer decrease until 1300 hr. after which it rises steadily, showing the highest peak of the day between 1700 and 1800, thereafter dropping rapidly.

The duration of social grooming bouts was very variable. In the sample in question the shortest observed lasted 28 seconds and the longest for 65 minutes, this latter was adult female - adult female dyad, and in fact was the longest grooming bout recorded in the entire study. The mean length of bouts in the period in question was 7.6 minutes. This was somewhat longer than the mean for all bouts for Group 1 recorded throughout the study which was 5.3, the range being from 17 seconds to 65 minutes.

After the termination of grooming bouts, and during the interval during which role reversal occurred, scratching of

Fig. 30

Percentage frequency of self-grooming and social grooming in Group 1 between 18.5.64 and 22.5.64.



the body fur with either the hands or the feet was very common. It is likely that this is partly a "displacement" scratching consequent on an approach-avoidance conflict, but probably also represents a rearranging of the fur after it has been disarrayed during grooming.

Involvement in social grooming

It was decided to investigate whether there was any age-sex class involved in social grooming either more or less than would be expected on an equal distribution of episodes between age-sex classes. The 129 incidents of social grooming shown in Table 20 and Fig. 29 indicated 258 involvements. In Group 1 at this time there were 3 adult males, 6 adult females, 2 subadult females, 1 juvenile male and two juvenile females. On this basis the expected number of involvements could be calculated on the basis of an equal distribution between different age-sex classes. This can then be compared with the observed frequencies and the significance of the differences calculated by means of a Chi-square test.

The observed frequencies of involvement of the different age-sex classes were AM 50; AF 104; SF 29; JM 12; JF 29. The expected frequencies were AM 55.26; AF 110.52; SF 36.84; JM 18.42; JF 36.84. The calculated value of Chi-square for these data was 6.43. There are four degrees of freedom, and the obtained value is not significant at the .05 level. The conclusion to be drawn is that age and sex status does not alter the probability of involvement in social grooming.

Social grooming partners

The involvement of each age-sex class with other age-sex classes in social grooming was estimated by taking the observed frequency of involvement of each age-sex class, and dividing this into an expected frequency on the basis of equal distribution between all age-sex classes. This was then compared with the observed distribution and the significance estimated by means of a Chi-square test.

Adult males were involved in 50 grooming episodes. On an expected basis the distribution between age-sex classes should have been AM 10.71; AF 21.14; SF 7.14; JM 3.57; JF 7.14. The observed frequencies were, AM 0; AF 39; SF 5; JM 0; JF 6. The value of Chi-square calculated from these data is 30.18. There are four degrees of freedom, and the value is significant at over the .001 level of confidence. The conclusion to be drawn is that adult males are involved in significantly more grooming episodes with adult females than would be expected on an equal distribution; they are also never involved in grooming episodes with other males.

The expected frequencies of involvement of adult females with other age-sex classes were AM 22.26; AF 44.52; SF 14.84; JM 7.42; JF 14.84. The observed frequencies were AM 39; AF 32; SF 13; JM 7; JF 13. The calculated value of Chi-square is 16.55. There are four degrees of freedom, and the value obtained is significant at the .01 level of confidence. The conclusions which can be drawn from these data are that adult females are involved with juvenile and subadult animals as frequently as expected, but are involved less than expected with other adult females and more than expected with adult males.

Subadult females were observed involved with age-sex classes in the following frequencies, AM 5; AF 13; SF 0; JM 4; JF 7. The expected frequencies were, AM 6.21; AF 12.42; SF 4.14; JM 2.07; JF 4.14. The value of Chi-square was calculated as 8.15. There were four degrees of freedom and the obtained value did not reach significance at the .05 level. The conclusion to be drawn is that subadult females are involved with all age-sex classes in the expected proportions.

The calculations for the juvenile male were complicated by the fact that there was only one of them in Group 1. The observed frequency was therefore only divided into four age-sex classes for the expected frequency per age-sex class. The degrees of freedom in the Chi-square were also reduced by one. The observed involvements were AM 0; AF 7; SF 4; JF 1. The expected frequencies were AM 2.55; AF 5.10; SF 1.7; JF 1.7. The calculated value of Chi-square was 6.38, which with three degrees of freedom was not significant. It must be concluded therefore that juvenile males are involved as expected with other age-sex classes.

Juvenile females were observed in 29 grooming bouts. The observed frequency with the different age-sex classes being AM 6; AF 13; SF 7; JM 1; JF 2. The expected frequencies were AM 6.21; AF 12.42; SF 4.14; JM 2.07; JF 4.14. The calculated

Chi-square was 3.64. There were four degrees of freedom and the obtained value is not significant. Juvenile females are therefore involved in grooming episodes with other age-sex classes as expected.

The conclusions to be drawn from the data on involvement are that although all age-sex classes are equally likely to be involved in social grooming, there are significant differences in the frequency with which certain age-sex classes are involved with each other. Subadult and juvenile animals are involved as would be expected, but adult females are involved less than would be expected with other adult females, and instead are involved more than would be expected with adult males. Males were never involved in social grooming with one another.

Invitations to groom by an animal were frequently not accepted. In the period illustrated in Fig. 29, 49 such invitations were refused Six invitations by adult males were refused, all by adult females. Twenty-eight by adult females were refused, fifteen by adult females and 13 by adult males. Three invitations by subadult females to adult females were refused. Six invitations by the juvenile male were refused, three by adult females, one by a subadult female, and two by juvenile females. Six invitations by juvenile females were refused, two by juvenile females, one by a juvenile male and three by adult females.

Mouthing

The close approach of another animal, especially of adult animals by juveniles often seemed to involve an element of fear, and under these circumstances "mouthing" was common. The approaching animal came up to the other animal in a slightly crouched position, often with the tail held horizontal. The approaching animal then put its mouth close to the other individual, and appeared to sniff the mouth. There was no vocalisation and apparently no change in facial expression by either animal. Throughout the entire study this posture was seen on 48 occasions. 27 of these were by juvenile females, 13 by subadult females, 6 by juvenile males and two by adult females. An approach of this type was never followed by attack, but the threat-face was occasionally given (13 times) and often the animal being approached either turned away or tried to prevent its mouth from being sniffed, but never actually moved away. On several occasions, as was noted on the section on day ranging, mouthing was used to identify the food another animal was eating. It is possible that it is a derived infant posture, as infants often sniff at the mouth of their mothers.

Lipsmacking occurs frequently in social grooming; but was not observed in any other activity, including copulation. It was used particularly by adult males to restart grooming by another animal after a pause during a social grooming bout. It was almost invariably successful in this respect. It was seen in this context in May 1964 on five occasions, performed by two different adult males; the groomer always resumed grooming the male.

Lipsmacking was observed in 72% of all females involved in grooming at some time or other during the bout. But its appearance and intensity were very variable. The appearance of the behaviour seemed to have nothing to do with the age-sex class of the animal being groomed, nor was it consistent or systematic enough to be related in any meaningful way with any scale of social differences. The precise significance of the behaviour apart from being indicative of a positive affectional approach is not fully understood.

Sitting close together may be legitimately considered as evidence of "friendly behaviour" in the natural environment where this is not necessitated by the presence of walls or wire, as it supposes some searching out of the other individual, or at least some synchronisation of movement. In the section on the stability of groups it was concluded that there was a high probability of adult males being found more than ten metres from another animal; this probability was low for adult females. Similar tendencies according to sex were also observed in juvenile animals.

In summarising the data on friendly behaviour, it can be seen that the positive affectional bonds between different members of the social group are rather complex. All members of the group are involved in social grooming, but adult males and adult females are involved with each other more than would be expected, which would tend to indicate a positive bond between adults of the opposite sex, especially in view of the fact that the adult

Lipsmacking was observed in 72% of all females involved in grooming at some time or other during the bout. But its appearance and intensity were very variable. The appearance of the behaviour seemed to have nothing to do with the age-sex class of the animal being groomed, nor was it consistent or systematic enough to be related in any meaningful way with any scale of social differences. The precise significance of the behaviour apart from being indicative of a positive affectional approach is not fully understood.

Sitting close together may be legitimately considered as evidence of "friendly behaviour" in the natural environment where this is not necessitated by the presence of walls or wire, as it supposes some searching out of the other individual, or at least some synchronisation of movement. In the section on the stability of groups it was concluded that there was a high probability of adult males being found more than ten metres from another animal; this probability was low for adult females. Similar tendencies according to sex were also observed in juvenile animals.

In summarising the data on friendly behaviour, it can be seen that the positive affectional bonds between different members of the social group are rather complex. All members of the group are involved in social grooming, but adult males and adult females are involved with each other more than would be expected, which would tend to indicate a positive bond between adults of the opposite sex, especially in view of the fact that the adult females groom each other less than would be expected, and adult males never groom each other. The data on copulation fall into a similar pattern. However, the data on group cohesion indicate that males are more likely to be found away from members of the group than are females. This indicates that males tend to be less attached to the group, and that females tend to seek the company of other animals, which must necessarily be females in many cases.

AGGRESSION

Ideas concerning the role of aggression and the expected incidence of it in primate groups are derived to a large extent from studies of captive populations, and specifically the study of Zuckerman (1932) on _Papio hamadryas_ in the London Zoo. The possibility that this behaviour was primarily a reaction to captive conditions and represented an attempt to adjust to conditions of ecological impoverishment was put forward in the introductory section. One of the first studies to cast doubt on the role of aggression in normal baboon social relations was the study of Hall (1962). Hall's main conclusions from a study of _Papio ursinus_ in the Cape of Good Hope Nature Reserve, South Africa, may be summarised as follows.

1. Inter-adult male aggression was rare. Of thirty-three recorded instances of chasing and chastising by this age-sex class, only one involved another adult male. No severe injury resulted from these incidents.

2. "Male 1" of S group was the aggressor against females on twenty-one occasions, and against other males and juveniles on eight occasions. These twenty-nine incidents were spread over 190 observation hours, about one incident for every six and a half hours of daylight.
3. Examination of female aggression occurrences shows them to be nearly twice as frequent as those of male aggression (110 to 57).

These observations on the baboons of the Cape Reserve are similar to the data obtained for the Lolui population of C. aethiops.

In view of the commonness with which adult males were attacked, it is not likely that the traditional concept of "dominant" and punitive adult male maintaining a "family unit" by means of threat and aggression applies to this population. The observations on friendly and sexual behaviour are incompatible with any "harem" type of organisation, as is the observation of adult and sexually capable adult males moving between groups, and the fact that males are frequently to be found more than ten metres away from another animal.

First it should be pointed out that the vervet population is not normally aggressive. Of a total of 1472 hours of observation on the island excluding territorial disputes and attempts at artificial feeding of Group 2, (which brings the observation time down to 1460.5 hours) a total of 423 inter-animal aggressive incidents was either heard or seen. It must be emphasised that there is a differential visibility of, for example, facial and vocal threats. Many of the former are likely to have been missed, whereas relatively few of the latter would have been. Nevertheless, this rather crude measure of aggression works out at only .28 of an incident per observation hour, even in the rather small territories of Lolui Island, and including all heard incidents. Threats to the observer were excluded from this analysis, although redirected aggression was not.

In the field it is often difficult to determine the precise proximal sources of threat and aggression. The first one often sees is the chase in progress, or the results of it. It should be emphasised that on only two occasions were animals observed to be caught and bitten as a result of an aggressive incident. Only one member of Group 1 (AF 4) was ever observed to be wounded, the incident was not observed, but a piece of fur was removed and there was a small abrasion on the exposed skin. Animals with serious bites were only observed three times in the entire study, one adult female and two adult males. Scarred animals were extremely rare.

Of the 423 aggressive incidents, the precise source of the aggression was only observed in 48 instances. Twenty seven of these were over food items, especially rather rare ones such as fungus, seventeen were caused by animals either jumping or falling near another one and being chased; three were the result of males attempting to copulate with unreceptive females; and one was by a mother with an infant one who chased a subadult who attempted to take her infant. There was no incident of aggression over sexual priority, and males were apparently not inhibited from copulating by the presence of another male, and were never attacked by other adult males when copulating.

A complete analysis of incidents where the aggressor and the victim were identifiable by age and sex category was carried out. A total of 108 of the 423 aggressive incidents met this criterion; the breakdown was as follows. Chases, attacks and fights 86, vocal threats without chasing 6, facial or postural threats without vocalisation or chase, 16. An analysis of these incidents shows that AMs were the aggressors in 21 cases, AFs in 46, JMs in 11 and JFs in 17. Adult males were the victims of attack in 46 cases, adult females in 17, juvenile males in 10 cases and juvenile females in 18 cases. The analysis of aggressors and victims is shown in Table 21.

The difference between the total in the above-mentioned Table and the total of identified chases is accounted for by the fact that twelve cases involved triads. Eleven of these were cases of adult females joining up to aggress against an adult male, and one was of two adult females joining to chase a subadult female.

For the purposes of testing whether there were significant differences in the frequency with which different age-sex classes were either aggressors or the victims of aggression, a Chi-square test was used. For these calculations all subadult females were considered as adults as much information had been obtained before this category was used. About half the identified incidents, 45

TABLE 21

Age and sex classes of aggressors and victims of aggression in dyads.

Aggressor	Victim	Frequency	Aggressor	Victim	Frequency
AM	AM	15	JM	AM	1
AM	AF	0	JM	AF	7
AM	JM	2	JM	JM	1
AM	JF	4	JM	JF	3
AF	AM	27	JF	AM	8
AF	AF	6	JF	AF	4
AF	JM	6	JF	JM	1
AF	JF	7	JF	JF	4
	Total	67		Total	29

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AF	JM	6	JF	JM	1
AF	JF	7	JF	JF	4
	Total	67		Total	29

in all, came from Group 1, which had an abnormal age-sex constitution, there being fewer males than the normal. In calculating the expected frequencies for the Chi-square test the mean of the age-sex ratios of Group 1 and the ratios for the rest of the population was therefore used. The mean percentage was AM 25, AF 41.5, JM 13.5, JF 20.

Using the above ratios, the expected frequencies of aggression by age-sex classes were AM 24, AF 39.84, JM 12.96, JF 19.2. The observed frequencies were AM 21, AF 46, JM 12, JF 17. The value of the Chi-square calculated for these data is 1.55. There are three degrees of freedom and the obtained value does not reach significance at the .05 level. The conclusion to be drawn is that no age-sex category is more likely to be an aggressor than any other.

However, when a similar analysis is made of the victims of aggression, the picture is very clear cut. The observed frequencies of age-sex classes being the victims of aggression are AM 51, AF 17, JM 10, JF 18. The expected frequencies, based on an equal distribution between all age-sex classes was AM 24, AF 39.84, JM 12.96, JF 19.2. The value of Chi-square for these data is 44.2. There are three degrees of freedom and the value is significant at over the .001 level. It may be concluded that adult males are much more frequently the victims of aggression than would be expected on an equal distribution hypothesis, and that adult females are less frequently the victims than would be expected. Juvenile animals are the victims at about the expected rates.

Artificial food sources and aggression

In an attempt to investigate the social effects of artificial feeding or "provisioning" Group 2 was fed with shelled peanuts which were scattered in an area where the grass had been recently burnt and which therefore afforded good visibility both to the monkeys and the observer, they were always placed in the same spot in the territory, within a circle of two feet diameter. (Plate 33).

The actual experiment was conducted in October, 1963, although pre-baiting had been carried out in August, the first two days in October were also used as a final training period, and observations on aggression were not carried out until the third day. There was no increase in the number of animals eating from the pile during the period in question. The calculations on the incidence of aggression at the pile were based on 11 hrs. 20 mins. when animals were actually feeding at the pile. The mean number of animals feeding at the pile through this period, being the mean of numbers observed at intervals of fifteen minutes, was 2.5 animals. The number of threats and aggressive postures which resulted in an animal leaving the pile was comparatively low; of 57 recorded instances of animals leaving when unsatiated, only 23 were chased or threatened. The other 34 left voluntarily without apparent threats from other animals at the pile. (c.f. Plate 33). These incidents of voluntary leaving were only considered when there were at least two animals feeding together. The number of aggressive incidents at the pile was approximately one incident every 29.5 minutes. This compares with the crude measure already recorded of .28 per observation hour. This is more than sevenfold increase, giving some indication of the

Plate 33. Group of two adult females with infant ones and a subadult female at the artificial feeding station. An adult male is just leaving the pile, although nuts are still available. No threat was observed, the precipitating factor probably being the actual number of females. Note the filled cheek pouches of the female nearest the camera.

distortion which may arise if artificial feeding is used as the normal means of social assessment without any attempt at obtaining quantitative control by studying a population which is not artificially provisioned.

Also significant was the high humber of animals leaving unsatiated but without being threatened; the voluntary leavers. Animals observed leaving in this manner were often not crouched, and showed no other signs of fear (c.f. Plate 33). This information is relevant to theories of social dominance as a means of social integration. If animals leave a tense social situation rather than being driven away, the motivational basis of this behaviour resides in the animal moving away and not in any dominance exerted by other animals. The basis may possibly be fear, but the evidence of the postures of animals moving away show that if this is so, only very slight fear is involved.

In order to establish whether any age and sex group was particularly likely either to be driven away from the peanut pile, or to leave it voluntarily, it was decided to compare the observed frequency of different age-sex groups leaving the pile with a theoretically expected figure based on an equal division between age-sex classes. In Group 2, which at this time included four adult males, five adult females, two juvenile males and three juvenile females, the expected frequencies with which age-sex classes left the nut pile were calculated as AM 16, AF 20, JM 8, JF 12. The observed frequencies were AM 16, AF 19, JM 7, and JF 15. The value of Chi-square calculated for these data was 0.925. There are three degrees of freedom, and the value does not approach significance at the .05% level. It may be concluded therefore that the probability of an animal leaving the pile or being driven from it is not affected by age or sex class. In order to decide whether either one of these two aspects, sex and age were in themselves important, two other Chi-squares were calculated, one for males and females, the other for adult and juvenile animals.

There were six males and eight females in Group 2 at the period in question. If the 57 incidents were to be divided equally according to the ratio of animals in each sex category, the expected frequency would be, males 24.4, females 32.6. In fact the observed frequencies were 23 and 34 respectively. The value of Chi-square for these data was calculated as .13. There is one degree of freedom and the observed value does not approach significance at the .05% level. It is possible to conclude therefore that sex does not influence the probability of being driven or leaving the nut pile.

By a similar method the group was divided into adult and juvenile animals, of which there were nine and five, respectively. The expected frequency, following a similar procedure to that previously described, was of 36.6 and 20.5 for adults and juveniles respectively. The observed frequencies were 35 and 22. The calculated value of Chi-square is .19, there is one degree of freedom, and the value does not approach significance at the .05% level. It may be concluded therefore that neither the sex nor the age of an individual has a significant effect on the probability of its either leaving or being driven from the peanut pile.

Further analyses of these data were made to see whether the same sort of conclusions could be drawn for the two types of leaving the pile by either being threated (t type) or voluntary leaving (v type). It is possible that a certain class of animals might habitually voluntarily move away in a tense situation in order to prevent aggression. The voluntary instances were first analysed. The observed frequencies of this type of behaviour (34 instances) were AM 9, AF 13, JM 6, JF 6. The expected frequencies on the other hand were AM 10, AF 12, JM 5, JF 7. The Chi-square value obtained from these data was .51. There were three degrees of freedom, but the obtained value did not reach significance at the .05% level, permitting the conclusion that voluntary leaving of the nut pile was not influenced by age-sex class.

Secondly, an analysis of the data for animals leaving the pile as a result of threat or chasing was carried out following the same procedure. There were 23 of these incidents. The expected frequencies were calculated as AM 7, AF 8, JM 3, JF 5. The observed frequencies were AM 7, AF 6, JM 1, JF 9. The Chi-square value of these differences was calculated as 5.00, which, with three degrees of freedom did not approach significance. It must be concluded therefore that age-sex class does not influence the probability of being driven from the nut pile.

Age-sex class is, as has been pointed out, a compound category, and further analyses were carried out of these two categories of behaviour, t type and v type to determine whether any particular one of the two attributes was important. The expected values for category v were males 14.5, females 19.4. The observed values were 15 and 19, respectively. The calculated value of Chi-square was .02, which did not approach the .05% level of significance. It may be concluded therefore that sex does not affect the probability of voluntarily leaving the nut pile.

A similar calculation was carried out for age categories of the group. The expected frequency for adults was 22, and for juveniles 12. The observed frequencies were the same, 22 and 12, and the value of Chi-square was accordingly nought, and the conclusion is permitted that age does not influence the probability of an animal voluntarily leaving the nut pile.

Similar calculations were then carried out for incidents in which animals were driven from the pile, to ascertain whether age or sex status influenced this probability. For sex categories the expected frequencies were males 10 and females 13. The observed frequencies were 8 and 15 respectively. The value of Chi-square was calculated as .70, which did not approach the value required for rejection of the null hypothesis. It may be concluded therefore that the probability of being driven from the nut pile was not influenced by the sex of the individual.

For age categories the expected frequences were adult 14.8 and juveniles 8.2. The observed frequences were 13 and 10 respectively. The value of Chi-square was calculated as .6, which for one degree of freedom was not significant. Age, therefore does not influence the probability of being driven from the nut pile.

In summary, the data from field observation showed that there were clear differences in the probability with which certain age-sex groups were attacked; adult males were particularly prone, and adult females had a certain amount of immunity. The data on artificial feeding gave a somewhat different picture, and emphasises even more forcibly the distorted picture of social organisation that may be built up from data obtained in this artificial feeding situation. At the nut pile there was no tendency for any particular age-sex group to attack any other, nor to be attacked. This means that the traditional concept of adult males having priority of access in the feeding situation does not apply to this population, even under conditions of social tension. All members of the group are equal in this respect. No animal either has priority because of age or sexual status, nor, on the other hand are animals persecuted for these reasons in the food-getting situation. It is possible, therefore that the tendency for adult males to be chased in the normal social patterns of the group, represents aggression not originating in disputes over preferred foods, but probably stemming from other social causes.

MATERNAL BEHAVIOUR AND MOTHER-INFANT INTERACTIONS

No actual birth of an infant was observed in the field. What evidence there was suggested that birth usually took place either during the night or the early hours of the morning. This was the case with the infant which was born to JF1 of Group 1 on the night of the 17th May 1964, and the one born to AF1 on 14.6.63. No evidence of discarded placentas was ever observed in the field and it is probable that the placenta is eaten by the mother; this was observed in a captive animal, and seems to be common throughout the Order. During the first few hours after birth the infant is held in a very close protective sitting position by the mother (Plate 29) and much cleaning behaviour, both of the infant and of the mother's ano-genital area is observed. This latter behaviour is often performed with one hand only, which is used to pick at the material adhering to the area, and which is often either eaten or dropped. After handling the vulva in this manner the sniffing and occasional licking of the fingers is commonly observed.

Adult females about to give birth were not observed to isolate themselves from the rest of the group. And after the birth there was a tendency for the mother to remain close to other animals, especially adult males, which showed no interest in infants and never attempted to take them from the mother. This tendency was most marked in AF1 of Group 1, who had her infant on the night of 14th June, 1963. Prior to the birth (i.e. between 5.6.63 and 13.6.63) she was not seen in close association with any adult male of the group. After the birth the picture changed dramatically, and between 14.6.63. and 29.6.63. she was generally to be found within 5m of AM1, and in grassland ranging and crossing in grassland between vegetation thickets she was generally within 3m of this male. It was interesting to note that the male did not alter his pattern of association with the rest of the group, and tended to move independently of it, and AFl kept close to him rather than with the rest of the group. It is possible that this behaviour in AFl was partly the result of the presence of the human observer, because although the group was becoming habituated at this time, it had not become completely used to his presence. When JFl had her infant the same tendency was noted, although not as strongly as in AFl the previous year. In August 1963, when four other adult females of Group 1 were carrying infant ones, the pattern seemed somewhat different, and no seeking of male company was noted, although there was a tendency for the females with infants to be found in fairly close association with one another, but no more than was usual at other times of the year. It is possible that the seeking of male company by mothers only occurs with the first few births of the season when adult and subadult females show a keen interest in the infant and attempt to take it from the mother. This interest in other infants declines sharply in females who have their own to look after.

The infant is capable of clinging onto the mother's fur very shortly after birth, but they are not always capable of finding the right position on the mother's ventral surface and have to be helped by the mother in this respect. The grip which the infants use is very characteristic, and provides the maximum support.

Plate 34. Typical ventral clinging position of an infant one. Grip is maintained with both hands and feet and the tail is curled over the mother's. This position is characteristic both when mothers are walking in the grass and along branches, or when sitting down, although the grip of the feet is often released in this latter case.

The fur is taken between the fingers which are then held close to one another, the fingers are then closed onto the palm, and the fur is also gripped in this manner, so that the grip is maintained both between and with the fingers. The tail of infants is also slightly prehensile at this early stage, and often passes between the mothers legs, and is curled over her tail, although this cannot give a very strong support. (Plate 34).

There are marked individual differences in the relative protectiveness of different mothers towards their infants, which makes the construction of "norms" of maternal behaviour a difficult and somewhat innacurate task. AF1, for instance, did not allow another female to take her infant until it was 14 days of age, whereas JF1 allowed her infant to be taken and held by other females for short periods as early as 2 days after birth. There was evidence that this was not correlated with the experience of the mother, as AF1 was multiparous and JF1 primaparous.

Infant Cercopithecus aethiops are born with a dark brown, almost black pelage, with a reddish pink face and ears. It is likely that this is the main differentiation affording them a privileged social position, making them immune from aggression, and a centre of interest for other females. There are probably other factors as well, such as size and gait. Dark infants were never the victims of serious aggression, and approached even adult males, pulling their fur and examining the scrotum with impunity. The interest of other females, especially subadults, in infants particularly at the beginning of the birth season, was intense, and many attempts were observed by animals attempting to get close to the infant and examine and/or handle it. Much maternal behaviour is therefore classifiable as protective behaviour, and much of the remainder being concerned with the physical welfare of the infant.

During the first month of life the majority of the infant's time is spent in close ventral contact with the mother, either suckling, or asleep, or looking around. During the first two weeks of life the "protective posture" of the mother is very pronounced, and one arm is generally held round the neck of the infant, and the other round the lower part of the body. For the first week of life AFl's infant was held in the ventral maternal protective position for a mean number of 54 minutes per observation hour, during the second week this had reduced to 47 minutes. JFl, on the other hand, only held her infant for a mean of 46 minutes per observation hour during the first week, and 39 minutes during the second. It will be noted from Fig. 31, that even though the maternal protective position is not maintained, contact with the infant may be. These figures give some idea of the variability between different females even in the early stages of maternal behaviour. When an infant is enclosed in the protective maternal position it has little chance to exhibit very variable behaviour, the three commonest observed are suckling, sleeping and looking-round. In the field suckling can rarely be distinguished from mere nipple-holding.

The amount of time spent in close contact with the mother decreases from birth, and the amount spent in contact with others increases. The first signs of relaxation of the tight maternal hold is observed, when infants sit on a rock or branch between the mother's extended legs. Suckling is still continued in this position. At between three and four weeks of age the mother was first observed to move more than two feet away from the infant. At the first sign of danger, or of the infant moving further away, the mother would run back to the infant and put it in the ventral position, or pull it back by the tail. By four weeks the infant will attach itself on receiving the stimulus of the mother's arm round its neck.

At two months of age the infants are very mobile. Much time is spent in running and gambolling, and also in climbing, but at this age they are still only rarely found in association with other infants for more than five minutes at a time. Most association with other animals is "aunt" behaviour by adult and subadult females. By two months the first, and largely non-aggressive refusals of the mother to the infant are observed when the latter attempts either to suckle or to attach ventrally. In these cases the mother merely avoids contact and does not actually push or bite the infant.

By five months of age the infants spend most of their day in the play groups (Plate 36), and markedly aggressive refusals of infant approaches are observed by mothers. The rebuff may be merely a push, but may take the form of a swift bite. At this age distress squeals of infants are occasionally not responded to by mothers until they have persisted for two or three minutes.

By seven months more aggression is shown by mothers towards the infants, and rejection is common. Ventral carrying is still occasionally observed, and in fact continued to 12 months of age, especially when crossing grassland. At this time the infants are large and can only be carried ventrally with difficulty, causing the mother to move with a peculiarly waddling gait.

It was interesting to note that infants were still "attractive" to subadult females up to eight months after birth; long after the infant pelage had changed to the characteristic adult colour. This behaviour was only occasionally observed and did not have the intensity of that observed during the first few weeks of life. The behaviour observed on these occasions varied between grooming the infant, putting it ventral, and occasionally a low-intensity version of grapple-and-bite play.

Although no information was available, it seems likely that the final severance of the mother-infant relationship occurs with the birth of the next infant. In the field it was impossible to obtain information because no adult female was observed to give birth twice. In the laboratory at Bristol it was the birth of a second infant to a female Erythrocebus patas which resulted in the final rejection of the infant. When the first infant, which was almost two years old at the time of the second birth, approached the mother, he was subjected to relatively severe threats and chastisement. However, if the juvenile was attacked by any other member of the group the mother had no hesitation in attacking the aggressor.

Maternal behaviour is a highly skilled performance, and there is ample evidence that although the basic patterns may be innate, the behaviour is subject to the normal rules of learning. It is clearly necessary, for the success of the species, for an adult female to be fully capable of dealing with an infant by the time her first one is born, and this explains the adaptive significance of "aunt" behaviour (c.f. Rowell, 1963). This behaviour was well marked in the Lolui population of C.aethiops. The most intense interest in infants was shown by subadult females, and the most persistent attempts to take them from their mothers were made by this age-sex class.

Attempts to take an infant from the mother were occasionally made directly without any prior involvement of the mother in social grooming. Occasionally if the mother was standing quadrupedally being groomed, the animal intending to take the infant would approach and pull the infant off. If the infant resisted or the mother objected, a certain amount of force would occasionally be exerted, and infants were often heard squealing when they were being pulled in this manner. More usually the putative aunt would in the first instance approach the mother and attempt to groom her, gradually working closer to the infant. Often in these cases there would only be an inspection of the infant or a slight grooming of it whilst it was in the ventral position. Often the infant would be lifted by the tail, whilst still retaining hold on the mother's fur with the hands, so that it came away hinge-like, and would then have its genitals inspected by the groomer. Genital inspection was generally both visual and olfactory.

Subadults that did succeed in taking infants were frequently very clumsy. Infants were occasionally observed being carried upside down, with the head in the groin of the aunt, and were often carried too low, with the result that they could not obtain a satisfactory grip on the fur of the aunt and had to be supported while she walked by one hand under the back. Another common mistake was to clasp the infant with its back towards the ventral surface of the aunt, so that it had to be supported with an arm underneath it. The general behaviour observed in aunts was a tendency just to carry the infant ventrally, and then to sit and groom it, and inspect the genitals; the behaviour is exactly similar to that of mothers, but no attempt to suckle or to attach to the nipple of an aunt, either adult or subadult, was ever made by an infant.

Aunts were very tenacious in holding onto the infants they had taken. On one occasion JF2 took the infant of AF2, then about three weeks old, and retained possession of it for one hour fourteen minutes, by running away at every incipient approach of the mother. Infants were often also heard squealing when mothers attempted to take them back because the aunts tended to hold on to them.

Very occasionally juvenile females would act as aunts, and their behaviour would be similar to that of subadults except that they were generally too small to carry the infants for long distances. These females occasionally engaged in play with the infants, generally of the grapple-and-bite type, although this was rare.

Infants were frequently observed "mouthing" the mother when she was engaged in feeding, although this was a characteristic chiefly of older infant ones and of infant twos. They were also privileged in that they were permitted to take food from the mother without being threatened, but as the infants became older, the chances of threat increased. By three months of age almost all the food required by infants was obtained from their own foraging, and very little from suckling.

The presence of infants in a group acts as a very strong cohesive influence on the females of the group. No male was ever shown to exhibit any interest in an infant, although they were tolerant towards them. Aunt behaviour was also important in that it gave animals practice in the handling of infants before it was biologically necessary for them to be fully competent. JFl on the birth of her first infant was able to deal satisfactorily with it, although for the first two days she had difficulty in keeping it in the correct ventral position, and she consquently had to support it with an arm whilst walking; but after this time she was as competent as any other mother.

INFANT SOCIAL DEVELOPMENT

The social development of infants is a remarkably rapid phenomenon, progressing from a complete dependence on the mother to a remarkable degree of independence in a comparatively short period. The behavioural and other characteristics of development proceed at approximately the rates shown.

First week.

The infant is completely dependent on the mother, and spends most of the time in ventral contact with her, sleeping and suckling. "Headweaving" in attempts to locate the nipple are observed, and the infant is able to support itself unaided on the ventral surface of the mother soon after birth. Looking round, both up at the mother and out at the external world are observed several hours after birth. By the end of the first week the first, weak escape attempts are seen, the infant kicking with the hind legs. But close contact is rarely broken at this stage.

Second week.

The reddish-pink of the face has changed to a greyish pink colour, and the contact with the mother is less restrictive. Infants are seen lying between the mother's outstretched legs on a rock. Escape attempts by the infant are stronger, and it may be pulled back by the tail if it attempts to move off. The first unsteady steps were observed during the second week. The hind legs are bent at the knees and give way frequently with the infant falling over. Underarm support by the mother in ventral carrying is less frequently observed than during the first week, and infants were observed not being in contact with the mother for periods of up to five minutes.

Third week.

The face is now predominantly grey, and the fur of the forehead is grey rather than the natal brown colour. Much interest is shown in things going on around it, both monkey and non-monkey. Breaking of contact with the mother is more frequent, although still for fairly short periods. Contact may be broken up to six times per hour, with the duration of each period up to six minutes long. (Fig. 31). Walking is steadier now, and animals fall over rarely, but the hindquarters are kept low and the hind legs are still bent. Animals of this age are able to scratch themselves with their hind leg in a co-ordinated manner. They show the beginnings of the typical infant bouncing run, with the tail curved up. Grass, leaves and berries may be put into the mouth at this age, but no evidence of actual eating was observed. The first signs of infant play-interactions occur during the third week, infants touching each other and bouncing away again.

Fourth week.

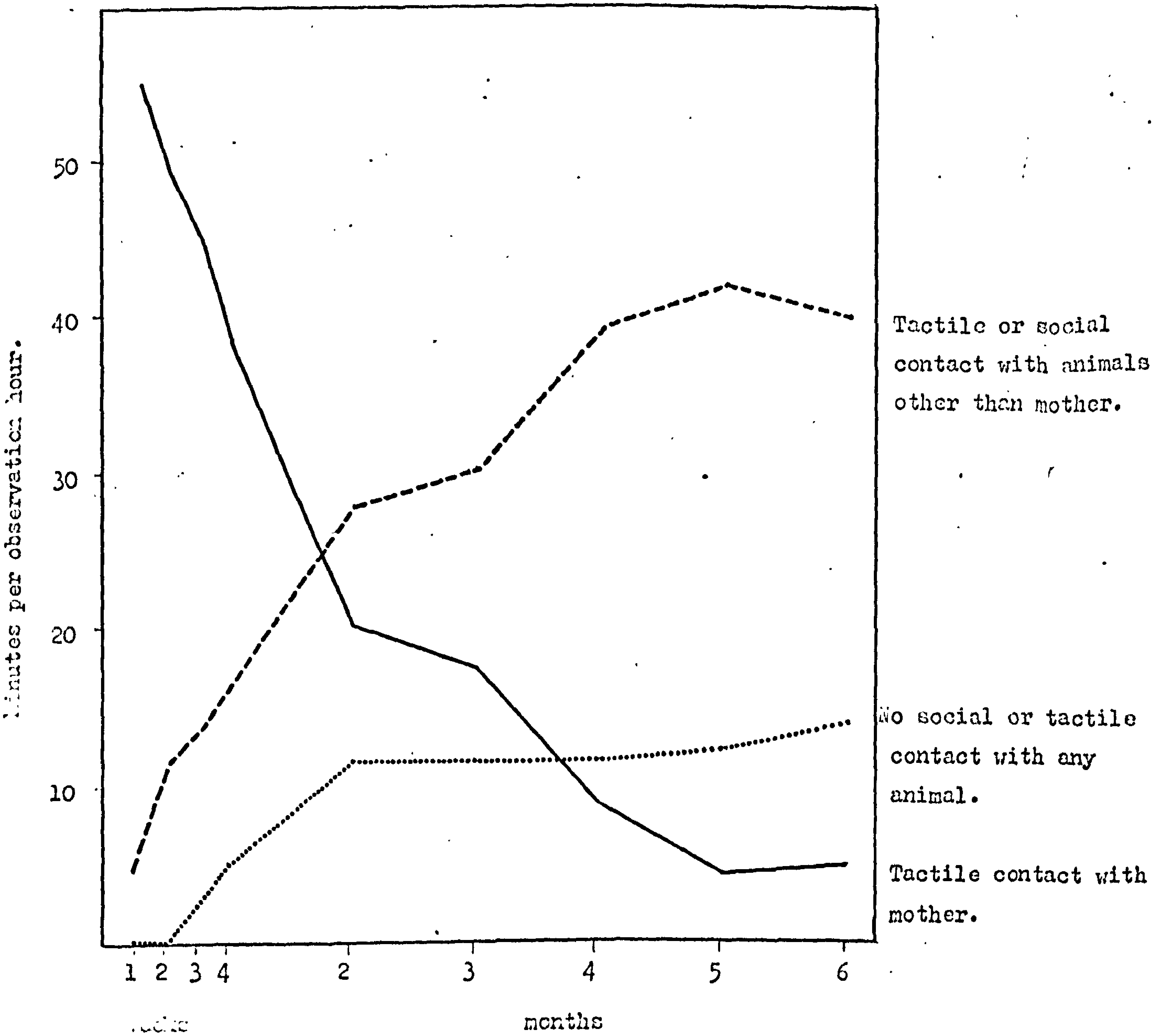
The mother may move five or six feet away from the infant, who is by now a capable walker and climber. At this age they can hang upside down from branches, holding on with their feet. The first instances of actual eating of vegetable matter, as distinct from merely putting it into the mouth were observed during the fourth week.

Second month.

During the second month infants may follow the mother in grassland ranging without being carried ventrally.

Fig. 31

Social development of infants: time per observation hour spent in certain activities.



Biting and eating of leaves, grass and berries is now fairly common. At this age the lighter brow band is quite clear. The face is covered with a yellowish grey down. The ears are grey and show no signs of pink, and the fur of the top of the head is beginning to turn the adult colour. The hind legs are no longer bent when walking, Infants of this age can run quite well and keep up with adults and juveniles running at medium pace.

The first evidence of real rejection on the part of the mother, and avoidance of the mother by the infant occurs at this age. But the mother is still the main source of refuge when any danger threatens. A relatively large amount of chewing dead twigs and sticks appears at this age, possibly indicating that teeth are being cut. Standing on the hind legs to inspect the surrounding environment is also observed for the first time during the second month. Interactions with animals other than the mother increase both in frequency and the variety of interactions. Touching other animals is common. At this age the interest in the human observer began to be observed. Sniffing at the perineum of other animals, not only the mother, was observed at this age. Very rudimentary grooming movements were also observed, although these were of very short duration, only one or two movements at the most, and could not properly be classified as grooming.

Third month.

The first chitters at the human observer were noted at this age, although interest in him was still very strong. The first bob-and-bounce threats were observed at three months. The fur of the wrists and ankles was beginning to turn to the adult black colour and the majority of adult foods were being eaten at this age, such as *Saba* fruit (Plate 35) *Saba* flowers were also observed being eaten. The sniffing of the perineal region of other animals was now a very common occurrence, although still no proper grooming was observed. At this age an interest in adult males began to be observed, infants approaching them either when they were lying being groomed, or sitting, and touching the genital area, particularly the blue scrotum. No adult male was observed to object to this, although they were clearly not stimulated by it in any way, and took very little notice. The start of play-groups was observed at this age, although they did not develop properly until later. Still no proper grooming was observed.

Fourth month.

Some of the more specialised food gathering habits are now observed. Lake-flies caught in cobwebs, for example, and insects are sought out, although no searching amongst dead leaves for cocoons or papae was noted. The chirrup vocalisation was first heard by an infant of this age. Suckling now may occur without ventral attachment, the infant sitting on a rock or branch facing the mother. Picking at the ano-genital area of other animals was noted, but still no behaviour that could properly be classed as grooming.

Plate 35. Three month infant eating Saba florida fruit. Note the comparatively light colour, and the fur of the hand and wrist beginning to turn black.

Plate 36. Play-group of five month old infants. The play which had been in progress was jumping from the branch on the left of the picture to the ground, climbing back and then repeating the activity.

Mounting of other infants was observed, but without erection.

Fifth month.

Infants are now properly classifiable as infant twos. Their colouration is identical with that of adults, they are mobile and efficient in climbing and jumping; mounting and pelvic thrusts were observed. This age-group is more orientated towards its peers than its mother, the fudamental criterion for classification as as infant two. Involvement with the mother may now be as little as 7 minutes per observation hour. (Fig. 31). Clumsy grooming movements are made, of short duration. Infant play-groups are observed at this age (Plate 36).

Sixth month.

Self-grooming is observed at this age, and is indistinguishable from that of adult and juvenile animals. Mounting, with erection and pelvic thrusts and the characteristic back-nuzzle is observed. It is doubtful whether penetration of the vagina is ever achieved, however, and no ejaculation or ejaculatory pause was observed. The territorial vocalisation, "aggressive-trill" is first heard at six months. Suckling, and occasional ventral carrying still occur.

Seven months.

At this age the searching of dried, dead curled leaves for pupae was first observed, and the adult method of catching insects by a hand clapping movement is observed. Insects and arachnids are a preferred diet item at this age. (Plate 37). Aggressive squeals and guttural grunts were first heard at seven months. The gallop leap was also first observed at this age, and presenting for grooming in the normal adult manner also appeared for the first time. Much interest was paid to the environment, looking-out alone and not in association with the mother first appeared at seven months. The canines were prominent, although still small and suckling was still occasionally observed, although it is doubtful whether any milk was in fact taken. Return to the mother was periodic, but generally occurred after bouts of playing; rejection of the infant by the mother was common, and often rough, pushing and biting being occasionally observed. In spite of this, these animals were still sought out by subadult females who attempted to groom them and occasionally hold them ventrally. Grooming of adult males by infants was first observed at this age.

Nine months.

At this age lipsmacking was observed in approximately the adult manner and duration. Grooming was indistinguishable from the pattern observed in adults. Suckling was occasionally observed, and in fact persisted until 11 months of age. Ventral carrying of infants was observed up to one year of age. It is probable, as has been described, that the final cause of the rupture of mother-infant relationships is caused by the birth of the next infant; by 18 months of age this will have occurred with many infants. They are classifiable as juveniles by this age.

Plate 37. Seven month old infant two. Infant has spotted an insect on a leaf above his head and slightly in front of him, and is about to kill it with a hand-clapping movement above and in front of head.

Quantitative data

Fig. 31 shows quantitatively the social development of the infant during the first six months of life. The data for the first two weeks of life comes from Group 1, and only two individuals were observed, and it is therefore the least reliable. The other data comes from groups in all parts of the north-west peninsula, and each line represents the mean of scores for between six and nine individuals.

These data indicate that tactile contact with the mother drops rapidly between birth and two weeks of life, after which the slope becomes more gentle, but by six months less than five minutes per hour are being spent in tactile contact with the mother. The data for social or tactile contact with other animals, which covers both "aunt" behaviour and infant play, shows that this increases fairly rapidly and consistently up to five months of age, followed by a slight decrease. At five months of age, when play-groups are common, as much as 40 minutes per hour may be spent in contact, either tactile or social, with other animals. The data for the infant being alone and not involved in any social or tactile contact shows that it does not occur until the second week of life; at this stage escape from the mother is likely to result in being taken by an aunt. But after two weeks the behaviour rises steadily to two months of age, when just over ten minutes per hour may be spent alone, after this age the rise is slow, but apparently steady.

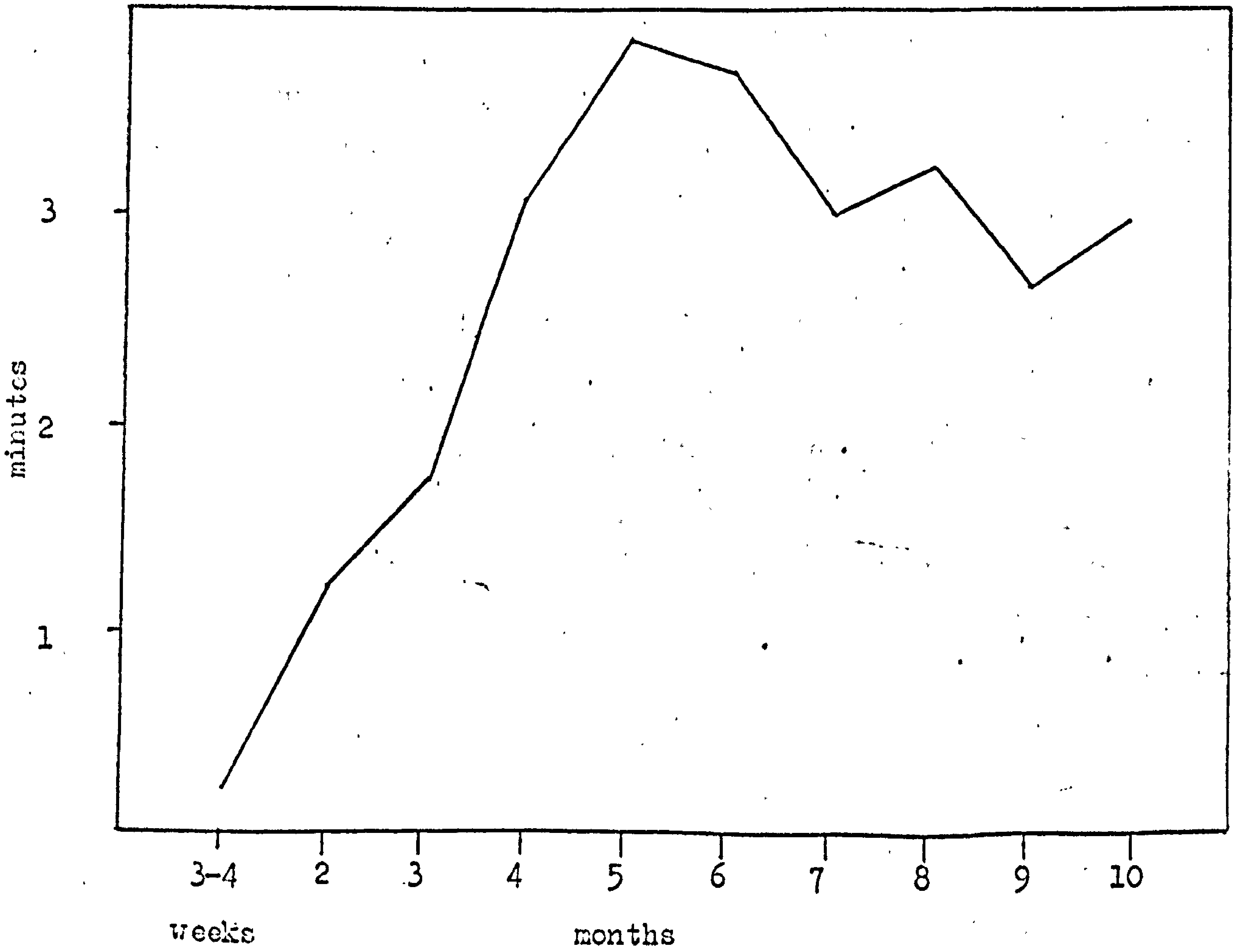
SOCIAL PLAY

The beginnings of social play arise during the first two weeks, when infants are still held in a tight maternal embrace by the mother. The infant looking round takes an interest in the surrounding environment, and particularly in moving objects and other infants. The first actual physical contact with other infants was observed during the third week of life, but was generally extremely brief; the longest encounter between infants observed by four weeks of age was 35 seconds, and the mean duration was only 14 seconds, (Fig. 32). Infant contact at this age was generally a tentative approach followed by a touch and then a rapid moving away in the characteristic gambolling or bouncing manner.

The duration of periods of interaction with other infants increased rapidly from one month of age (Fig. 32). Most of the play patterns observed appeared at approximately the same developmental stage except for chasing which was the earliest. The mean duration of periods of interaction reached a maximum during the fifth and sixth month of age. The three patterns of social play observed were chasing, play biting, (which graduated into a more intense version including wrestling, called grapple-and-bite), and chain jumping. These behaviour patterns were well differentiated by two months of age, at about the time when interest in the human observer began to be shown by infants. This suggests that there may be some relationship developmentally between exploration and social play.

Fig. 32

Mean duration of infant-infant social contact interactions.



Chasing is the first play pattern to develop and also the first to disappear. Short play chases are seen in three and four week old infants, but are only rudimentary and involve no more than two or three bouncing steps. Play-chasing is distinguished from aggressive chasing by both developmental and behavioural criteria. No chase that could confidentaly be assigned to aggression was observed in infant animals. The distance between the chased animal and the chaser tended to remain constant, the chaser making no attempt to actually catch up with the object of the chase. Actual capture was often by the chased animal turning round and facing the chaser. The encounter would lead to a play-bite or grapple-and-bite session. Play chasing often involved several circuits of obstacles such as rocks or anthills, grass tussocks or saplings, which aggressive chasing never did. The posture of infants involved in chasing was characteristically upright and bouncy, and very distinct from the crouched position of an aggressive chase. The facial postures involved in aggressive threat were also never observed in play-chasing.

Play-biting was the inevitable consequence of a play-chase session lasting for more than a few seconds. If the chase had been stopped by the chased animal turning round, generally the animals clasped one another, face to face, and bit each other on or around the head or shoulders. It was rare for arms, legs and tail to be bitten in play-bite sessions. At higher intensities rolling over and wrestling was observed. This was called grapple-and-bite, and involved a higher level of excitement. On three occasions three month old infants were seen with penile erections when involved in grapple-and-bite session; this is a common accompaniment to excitement in juvenile and adult males. The biting in these two play patterns was inhibited, the mouth was opened very wide, but not closed very far.

Chain-jumping appears by two months of age; the infants find a convenient branch which hangs downward and ends about three feet or less from the groumd. They then descend the branch in single file, and jump off the end to the ground. They then usually climb up the tree or shrub again and repeat the behaviour. A maximum of five successive circuits was seen in an infant in Group 1. Saba florida and Alchornea cordifolia are the commonest sites for this behaviour, as both have supple, pliant branches which either bend over easily or normally hang down close to the ground.

Play is punctuated by returns to the mother. During the first two months of life a play incident such as chasing, but more commonly play biting, will be terminated by the mother coming up and taking the infant away, or the infant may run off and find the mother. Gradually this tendency becomes less marked (Fig 32) and by five months the duration of each incident reaches a maximum and is punctuated by relatively few returns to the mother. Individual recognition of most infants was not possible, and it was therefore impossible to state whether there was a tendency either for any infant to be particularly involved or otherwise in play behaviour, or whether any animals were more likely to be chasers than were others. The impression one obtained was that this was not so, and on the high number of reciprocated chases, i.e. role reversal between chaser and chased animal, suggests that this is not so. Of 47 play chases where it was found possible to keep trace of the identity of chaser and chased animal through the play-bite session, nineteen showed definite role reversal in the chase immediately following a play-bite session, and a further seven showed it in a third chase. The fact that all infants of Group 1 played in a single play group, suggests also that there were no animals less involved in play than were others.

Play-chasing has virtually ceased by seven months of age. Grapple and bite behaviour is also rarely observed after seven months of age, although play-biting continues for much longer, and is also observed in juvenile and subadult animals, especially if they are involved in play sessions with infants as occasionally happens. Chain-jumping has also ceased by seven months.

It is not possible to state from a field study of this nature the basis of the decline in play behaviour. It corresponds in the behavioural repertoire to a change from exploration and interest, to the relatively high levels of aggression characteristic especially of juvenile males. The problem of the precise causes of the decline awaits detailed experimental investigation.

TERRITORIAL BEHAVIOUR

The problem of the existence of territorial behaviour in the higher primates is one which stems partly from Carpenter's early work and is partly the result of sematic confusion, and in part the result of conflicting evidence. Burt's (1934) definition of territorial behaviour has already been mentioned, and by these criteria there can be no doubt that the population of Lolui Island is strongly territorial. It is not presumed that this behaviour is characteristic of the entire species group; in fact the population observed at Chobi certainly was not, but it is postulated that the species is capable of showing territorial behaviour under particular ecological conditions, crowding such as was observed on Lolui being one of them. In this respect the species is capable of adjustment to particular environmental conditions.

The behaviour patterns to be considered as territorial behaviour may for convenience be treated under the headings of territory marking and territory defence, although in fact there is a considerable amount of overlap between the two.

Territory marking.

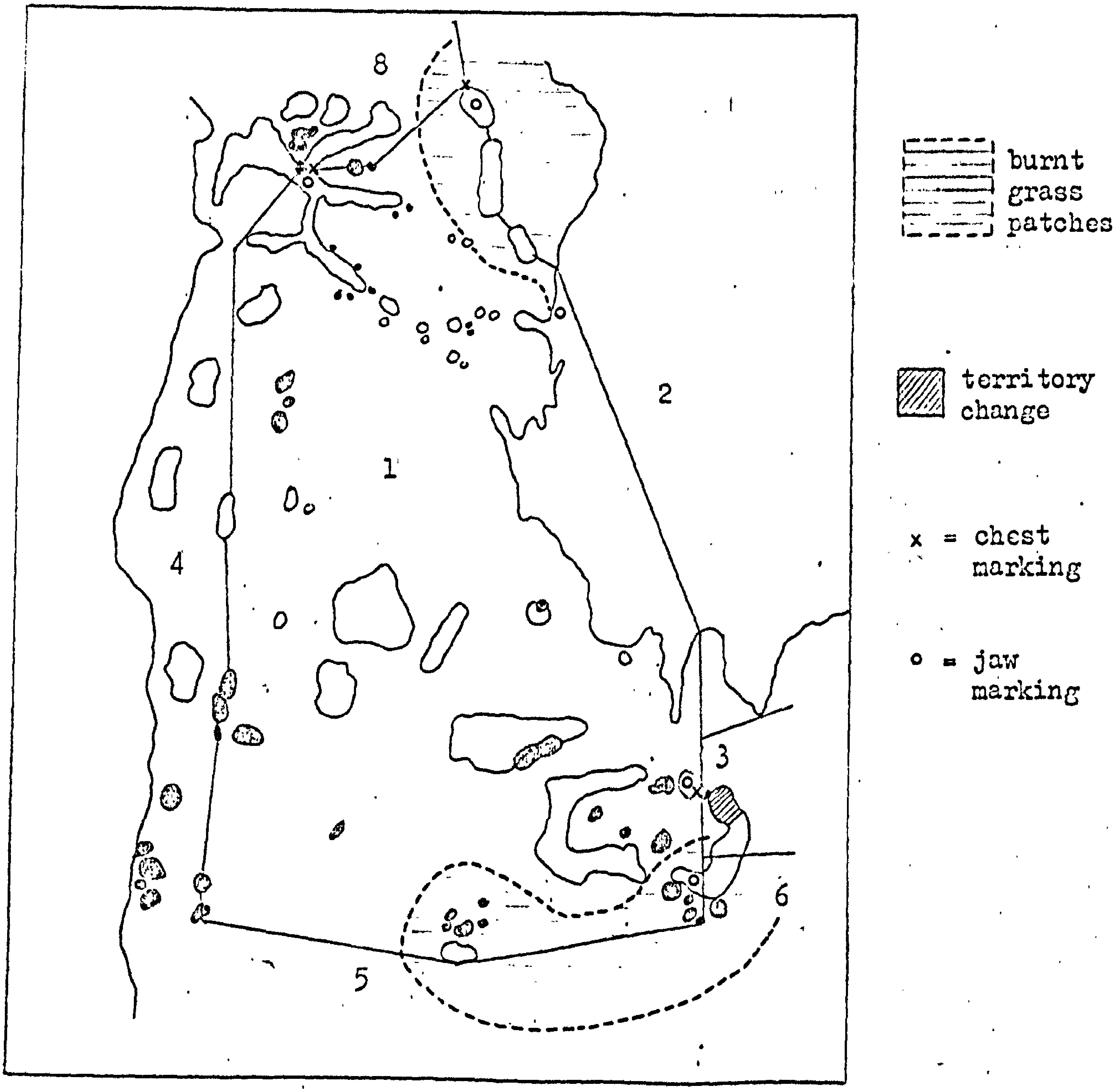
In view of the comparatively large role played by scent and olfaction in the day to day social and individual behaviour of the vervet monkey, it was not surprising to find that one method of marking territories was the scent marking of trees or rocks on the boundary of adjacent territories. The observation was perhaps more surprising in view of the fact that previously no scent marking of territories has been observed in any primate higher than the Prosimii. The observations made on Lolui have since been confirmed independently at the Johanesburg Zoo (M. Lyall-Watson, pers. comm) and in the captive group at Bristol. The observation was also surprising in that as yet no secretory glands are known on the chest or at the angle of the jaw, the two parts of the body used in scent marking. Histological examinations of the possibility of glandular areas at the angle of the jaw are however in progress at the Johannesburg Zoo, but have as yet yielded no positive results.

The concept of territory as a defended area is one that is open to criticism, in that it was clear from the Lolui information that this behaviour primarily involved the marking of objects, and in those areas where there were no objects susceptible to marking, such as areas of grassland which had been denuded by grass fires, ambiguities resulting in frequent inter-group altercations were common.

Low intensity scent marking, "jaw-marking" , was performed by both male and female group members, and was performed in the majority of cases on branches. It took the form of an alternate wiping of each angle of the mouth against the branch with a sideways and forward movement of the head. It was often observed in animals that had been sitting in a relaxed sitting position with the head resting against a branch or trunk of a tree (Fig. 28 B.). This behaviour pattern was seen performed 34 times by members of Group 1. The usual sites are shown in Fig. 33, and it can be seen that it usually occurs in the neighbourhood of territorial boundaries, and in fact was not observed more than 15 metres from a territorial boundary. It was observed five times in adult males, twenty-six times in adult females, and three times in subadult and juvenile females. On eleven occasions the behaviour

Fig. 33

Territory marking and sites of territorial disputes of Group 1.



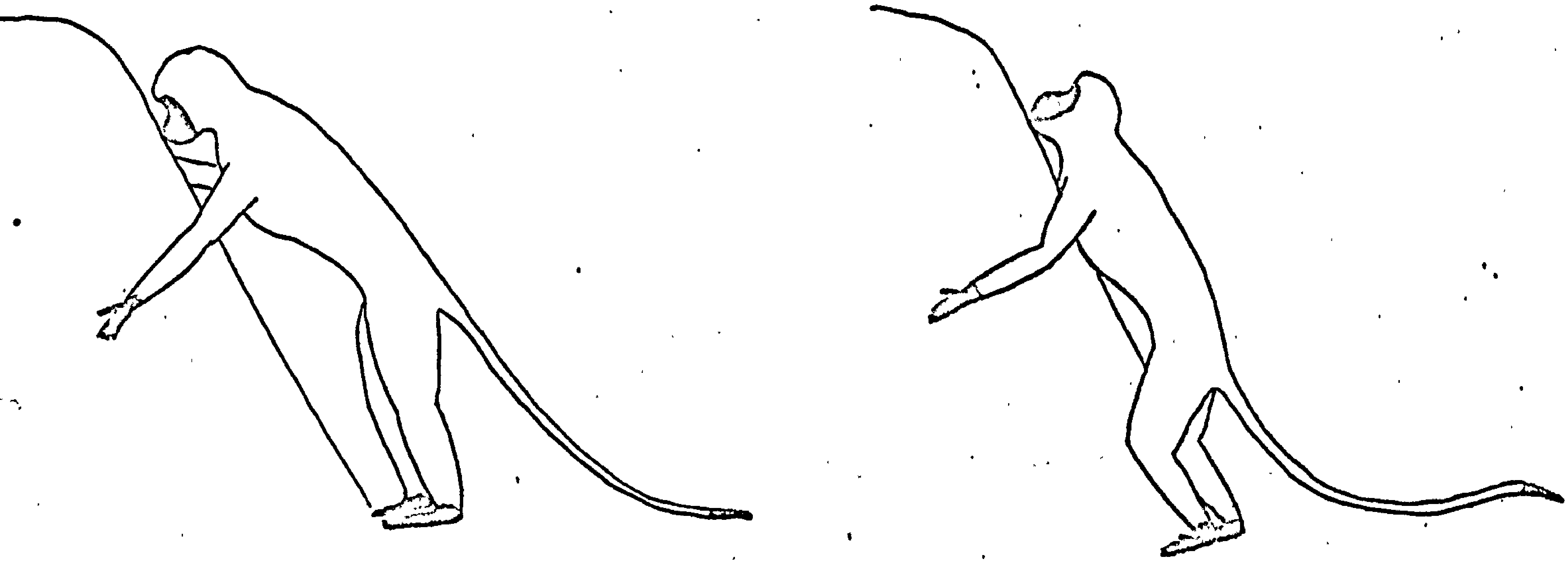
was seen either during or immediately after territorial disputes or chases. In the other cases no apparent stimulus was present.

No particular scent was discernible to the human observer on areas which had been marked in this manner, and on only three occasions was interest in such areas shown by other members of Group 1, which sniffed the area briefly. But no reaction to the markings was observed in trespassing groups, which always dashed back to their own territory on the approach of the human observer. It is possible, therefore, that markings were inspected by trespassers or intruders.

The second type of scent marking, "chest marking" was comparatively rare and was only observed seven times. It was performed twice by adult males and five times by adult females. The objects marked were generally branches, but on one occasion a rock was used. In this incident, which was performed by an adult male, the animal stood bipedally with arms spread wide and horizontal to the ground and chest close to the rock which was sniffed very slowly and carefully; the hindquarters were then moved away from the rock by the animal bending forward and bringing the chest into contact with the rock as close as possible to the ground. The animal then straightened up slowly rubbing his chest against the rock as id did so. Each rub was followed by a sniff, which was in turn followed by a sniff. (Fig. 34, A,B). When branches were marked, and this was observed in both male and female adults, the animal held itself very close to the branch with its arms round it and alternately sniffed and rubbed. The whole behaviour seemed particularly intense, little notice being taken of other animals or noises whilst it was

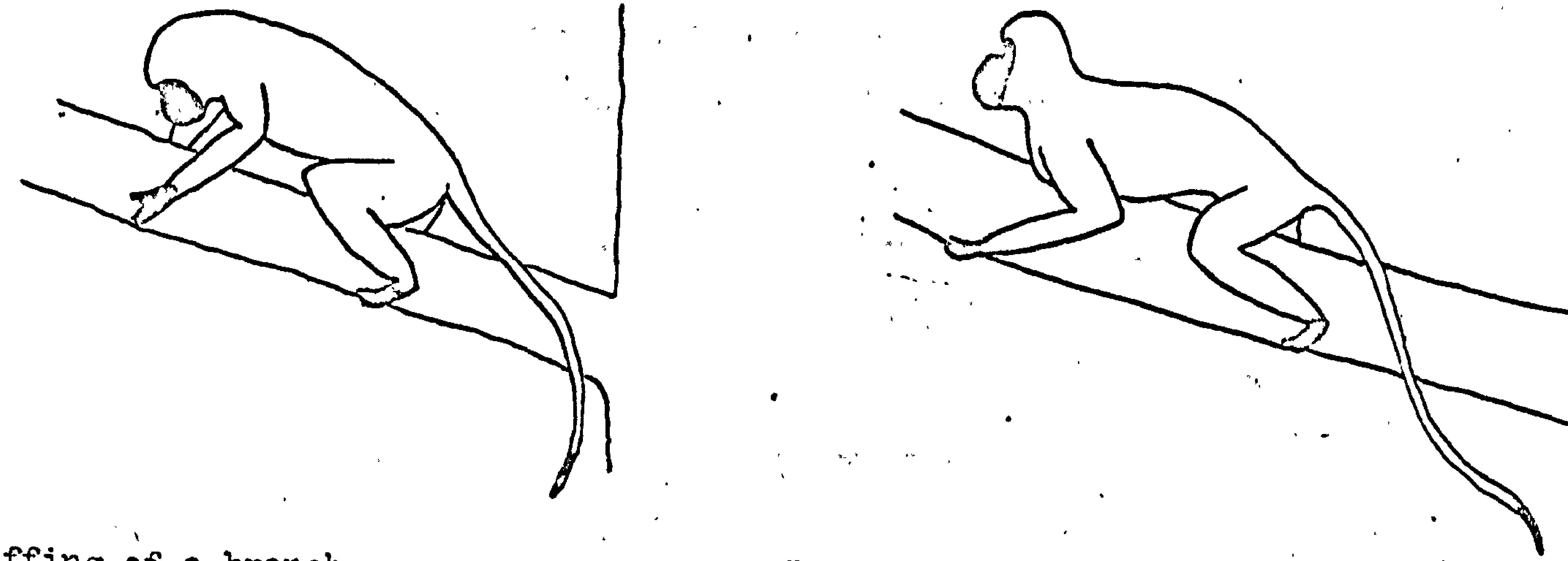
Fig. 34

Territorial scent marking with the chest.



A. sniffing of the rock

B. rubbing of the rock



C. sniffing of a branch

D. rubbing of a branch

in progress. Marking of this type sometimes continued for two to three minutes in an unbroken sequence. (Fig. 34, C.D.). The locations of objects marked in this manner (Fig. 33) were all actually on the territorial boundary, and were in fact boundary markers. The behaviour was only observed in animals that had been trespassing into another group's territory and had been chased back, or during territorial disputes with another group.

A behaviour pattern that was intermediate between territorial marking and territorial defence was the display known as "jumping round". This was only performed by adult males. Thirty-eight incidents of this behaviour were observed by Group 1 males, thirty-two of them being performed by AM1, the male who remained with Group 1 throughout the study, five by AM4, and one by AM5. The behaviour involved climbing to the crown of a high-canopy tree such as *Canarium schweinfurthii* or *Maesopsis eminii* and jumping round the perimeter of the crown, in big, noisy leaps. Branches and leaves were frequently broken in this display. The behaviour was usually terminated by a spectacular leap from the high canopy to the understorey, sometimes a drop of thirty or forty feet. A maximum number of two and a half circuits of the crown of a large *Canarium* was observed in this display.

The site of the display was necessarily restricted by available high canopy trees with a suitable crown, and although there was a tendency for it to be performed only in those areas bordering on adjacent territories, (it was never performed in the vegetation clumps in the centre of Group 1's territory for example), it was not closely associated with boundaries. The noise of this display always attracted the attention of other animals, even if only a quick glance at the source of the noise. It was also a socially infectious behaviour, and the performance of it by one adult male would often trigger off performances by males of neighbouring groups. It was sometimes associated with territorial disputes, but in 26 cases this was not so.

Territory defence

The defence of a territory involves primarily the detection of intruders and their expulsion. The detection of trespassers is performed by all age and sex classes and resembles exactly the behaviour towards the white human intruder. Chitters, chirrups and honks were all observed and played an apparently similar role. However, an animal coming on a trespasser unexpectedly at close quarters would frequently give the aggressive trill, which was only rarely given to the human intruder.

Trespassers were generally spotted by group members engaged in their normal patterns of day ranging and who then either chased them out or vocalised, calling the attention of other group members to the presence of intruders. The same hypersensisivity observed in reactions to the human observer was also observed in the juvenile male of Group 1 to inter-group trespassing. It is not as easy to obtain information on the initiation of aggression against monkey intruders as it is against oneself. Of the 23 incidents in which members of Group 1 chased out intruders from their territory, the initial alarms were observed in only seven cases, and in six these were given by the juvenile male. The other case was an adult female.

The behaviour of trespassers is very characteristic. If more than one animal is involved they keep very close together. The least dispersion of groups is observed under these circumstances. No looking-out behaviour was observed by trespassing groups, but vigilance was maintained by all members of a trespassing party, by frequently looking round. At the first sign of the approach of the territory owners the trespassers would generally rush back to their own territory. A group running away would often be extremely close together, on one occasion 13 members of Group 1 were observed being chased back from Group 3's territory, in a small knot, no more than a few inches between the various individuals.

A territorial chase of this nature stops when the group has crossed the boundary into its own territory. It then turns round, sits on available sites, such as rocks or anthills, faces the aggressors, which do not cross into trespasser's territory, and there then follows a session of mutual threatening, aggressive-trilling, threat faces, bob-and-bounce threats, which may last for up to half an hour. This is similar to the grassland disputes which will be described later.

As there is some social differentiation in the vigilance of different age-sex classes, juvenile males being hypersensitive, there is also a clear age-sex difference in the animals which are involved in chasing out intruding animals. Forty-two such chases were seen involving Group 1, in twenty-three they were the chasers, and in nineteen were chased. In thirty-eight of these forty-two incidents adult males were the principal chasers, and in twenty-seven of them two or more adult males were involved.

This is very different from the picture in intra-group aggression when adult males were never observed to join together in mutual aid. In only four cases were adult females the principal chasers, and in all of these intruders had crossed the line back into their own territory before the owner males had had chance to rearch the site of the altercation.

The role of adult males in territorial defence is seen very clearly in grassland altercations, and when groups who have been chased out turn round and face their aggressors. The pattern which then emerges is for adult males to stand and face one another each in their own territory, with tail held vertical, exposing the red anal area, the white fur and the blue scrotum. There is much mutual threat facing, aggressive trilling, and honking by the males. The adult females and also to some extent the subadults and juveniles tend to cluster round the male, at his side and behind him, grooming him and interspersing the fast, frantic grooming with aggressive threats at the other group.

Grassland altercations only occurred in those areas marked in Fig. 33 where there had been recent grass fires, reducing the number of landmarks and increasing the ambiguity of territorial boundaries. These areas were also preferred areas for feeding, and groups in whose territory such areas occurred tended to spend much time during the day feeding there. If the burnt area crossed a territorial boundary, it was therefore almost inevitable that groups would be brought into close contact in an area of few landmarks. Twenty-three such disputes were observed involving

Group 1, eighteen of them in the area of the boundary with Groups 8 and 2, and five in the region of the boundary with Groups 5 and 6. All these incidents took place after the grassland had been burnt, but were not restricted to the time when the burn took place, or immediately afterwards. It was pointed out in the section on feeding that the new shoots of grass are a preferred food. Generally, the two groups fed without incident in the grassland until one animal crossed the ambiguous boundary and was chased out or threatened by a member of the other group. At this point the two groups would congregate in two sides, facing one another and threatening in the way described. The adult males were the focus of attention as in the previously mentioned manner. Males would make short rushes and would be chased back, and this rushing and counter-rushing would often continue for ten to fifteen minutes. The longest incident of this type was observed to last for 48 minutes, although varying in intensity during this time.

There was evidence, apart from the minor variations mentioned due to alterations in the physiognomy of the territory, that territories were remarkably stable. The only change which occurred during the year of study is shown in Fig. 33. During June 1963 Group 1 was trespassing into this area but was being invariably chased out. This continued, with increasing uncertainty of result, until May 1964, when Group 3 was invariably chased out by Group 1. The fact that this small area took almost a year to change ownership indicates the stability of territories. The area involved was also comparatively small, an area of thicket less than 20 metres by 20 metres.

The stability of territories is also reflected in that there was an extremely high probability, almost unity, that a trespassing group would be chased out by the group into whose territory they were trespassing. All the 42 chases observed are compatible with this observation. The only uncertainty was observed in the Group 1 and Group 3 territorial change. Group 1 was observed to chase out trespassers of Group 8 six times, Group 3 nine times, Group 2 four times, Group 4 twice, Group 5 once, and Group 6 once. Group 1 was chased out of other groups territories in the following frequences, by Group 8 eight times, by Group 3 seven times, by Group 2 three times and by Group 4 once. It will be seen from this that adult females who do not change between groups have a minimal chance of coming into contact with animals other than their immediate neighbours, and these contacts are invariably aggressive. This emphasises the importance of the interchange of adult males between groups in maintaining the genetic stability and unity of the population. Territorial behaviour, as has been pointed out, does not inhibit the interchange of adult males between groups in this population.

The incident of AM2, who left Group 1 and joined Group 8 has already been mentioned. This animal was not scarred and bore no evidence of any fights. It had not been observed in any fights prior to leaving, and was in any case probably the strongest of the adult males in the group. Yet within three weeks it was chasing out members of his old group who had trespassed into the new territory, and was standing and threatening AM1 and being groomed by Group 8 females in a grassland dispute. Adult males who trespassed with a group were always chased out, but it is possible that individual adult males may not be subject to the same aggression and chasing as are those with a group. AM4 and AM5 were not observed being chased except in the normal social patterns, i.e. by one or at most two animals, as distinct from the entire group. The example of AM2, and also those of AM4 and AM5 would tend to indicate that assimilation of new males is fairly rapid, and if they are subject to chasing and aggression, this may only occur over the first few days. No animal was ever caught and bitten as the result of a territorial dispute.

SUMMARY AND DISCUSSION

The increase in the number of field studies of primates over the last fifteen years has, until comparatively recently, not been associated with any comparable development from motivational theories of primate social organisation and structure. Motivational theories, it should be pointed out, are not incompatible with an evolutionary point of view, but the unitary motivational theories that have been common in primatology represent an over-simplified and over-intellectual viewpoint of primate social structure.

Two main motivational models have been used. The theory of sexual attraction and all year round mating as the basis of primate group cohesion was stated most cogently by Zuckerman (1932). This pioneer investigation raised an issue which has been susceptible to systematic and empirical investigation, and which has directly influenced the majority of subsequent field studies. Most of these have attempted to obtain information about the periodicity or otherwise of mating behaviour in order to establish the adequacy or otherwise of this theory as an explanation of the facts of primate social structure. The most comprehensive review of the information available up to the present was undertaken by Lancaster and Lee (1965). These authors concluded that constant sexual attraction cannot be a basis for the persistent social groupings of primates. These authors further claim that where copulation is restricted to a few months of the year, as in certain macaques, no variation in the strength of the social bond is observed.

The observations made on Lolui Island fit the growing body of information supporting the point of view typified by Lancaster and Lee, and indicating that sexual attraction cannot be the sole, or even in some cases, a major factor explaining primate social cohesion. There was an observed birth season on Lolui, with all births being concentrated between mid-April and mid-September. This was matched by evidence indicating that there was also a restricted season of copulation on Lolui Island.

The only evidence of the weakening of social bonds in this population was the interchange of adult males between groups, which occurred fairly freely. There was, however, nothing resembling a general breakdown of group structure, and the composition of groups and the territory in which they lived appeared to be remarkably stable. It seems likely that there are many factors promoting group unity and cohesion, and that sexual behaviour is only one of them. On Lolui Island copulation is much rarer than in the baboons, on which the theory of sexual attraction as the basis of primate group cohesion was based, and is entirely insufficient to support the hypothesis that this behaviour is the basis of the group cohesion. The one male which remained with group 1 throughout the study period was the one which copulated least. There was an inverse correlation between the length of time spent in the group and the number of copulations performed.

Recent attempts have been made to correlate group structure, population dispersion and species ecology. (c.f. Crook & Gartlan, 1966). These studies assume that group structure is not fortuitous, dependent only on the sexual appetites of the group members, but that it is an adaptation to the particular environmental conditions of the species or population, permitting efficient dispersal and utilisation of the environment. Crook and Gartlan (loc. cit.) concluded that in the widespread savanna and forest-fringe species, variations in social system were possible owing to the plasticity of intra-group relations possible in these forms, intimating that selection pressures may result in different social structures based on the interaction of learning and social cohesion on a multiplicity of motivational factors. The primate group, in other words, is determined by many forces and suceptible to modification by environmental or other changes. Both the uniformity of the phenomenon - the majority of primates living in groups regardless of the different frequencies of mating, (very common in baboons, extremely rare, for example in gorillas) - and the observed differences in structure tend to indicate that a simple motivational model of primate groupings is not sufficient.

Other social factors such as the birth of infants have considerable social significance and are almost certainly factors promoting group cohesion. The mother-infant bond may also persist, as may the peer-bond, making animals reluctant to move between different groups or to leave the one into which they were born, although there is as yet no definitive evidence on this point. The benefits of social groups, such as mutual grooming and defence against potential predators and intruders also probably play an important role. The animal in a group is generally speaking a "confident" animal, and Hinde and Rowell (1963) have demonstrated that the removal of an individual from the group, even though it may be kept within hearing distance of other group members, is a stressful situation.

Whereas the actual phenomenon of primate social congregations has often been explained with reference to a unitary "sexual attraction" theory, the actual structuring of the congregations has generally been explained with reference to the theory of "social dominance". This concept has been used in both a descriptive and an explanatory role.

As an explanatory concept, "social dominance" has altered with the passage of time and seems to have escaped the critical re-appraisal to which Hinde (1959) subjected the concept of unitary drives. In ornithological studies "dominance" has often been used descriptively with a clear operational definition, but this has rarely been the case with primatological studies.

The concept was originally raised to explain certain aspects of aggression and priority of access to need-satisfying objects in the captive situation. But mainly through the works of Yerkes (1939, 1943) and Maslow (1936) it came to be regarded and used as a motivational factor explaining the reliability of the outcome of dyadic interactions over objects such as food or access to sexually receptive females. As a result of this, different and distinctive behaviour patterns such as sexual behaviour and aggression came to be regarded as capable of motivation by a "social dominance" drive, as well as by their own "appropriate" drives. And with certain workers the concept of "social dominance drive" came to be regarded as a drive as powerful and fundamental as the sex drive.

The structure of social groups on Lolui Island, as in most other primate populations was complex, and there were well-defined social roles. Thus the care of infants was exclusively the province of adult females; no adult male showing any interest in, or care of an infant. Subadult and juvenile females are prepared for their role as mothers by the "aunt behaviour" which ensures that no adult female becomes a mother without having first had some prior experience in the handling of infants.

Vigilance was maintained by all age and sex groups, but particularly by juvenile and adult males. The juvenile males gave warning of the approach of non-dangerous intruders such as other groups trespassing into the territory. Adult males performed "looking-out" vigilance behaviour, and it is this age-sex class which is concerned with the defence of the group and the chasing out of intruders. The only observed instances of males of a group being in close proximity and co-operating in a common cause was in driving out members of an intruding group.

The evidence is that social roles of a group are dependent on several factors, of which age and sex are probably the most important. These roles all ensure the success of a group in the particular conditions of the habitat in which the group lives, and is probably modified if ecological or other conditions change. All roles are therefore likely to be important, otherwise they would be excluded from the social repertoire. Any social structure is therefore not likely to be easily or validly explicable in terms of a simple "dominance hierarchy".

The use of "social dominance" as an explanatory concept assumes a certain amount of interaction between group members in order to provide quantitative and reliable measures necessary for determining the "hierarchy". It assumes that there is aggressive competition over available commodities, such as food or receptive females. These conditions did not apply to the population of Lolui Island.

Interaction between adult males was a comparatively rare occurrence. The chasing of an adult male by another adult male only occurred when animals had recently joined the group. No male was ever observed to groom another, nor to mount another. No aggression between males was ever observed over copulation. Copulation was not inhibited by the presence of another adult male. Adult males tended to be found away from other group members and from each other. There was an inverse correlation between the number of "jumping around" territorial displays shown by an individual and the amount of copulation. Adult males, far from being aggressive and punitive, as the traditional "social dominance" theory would require, were the particular objects of aggression by other group members, especially adult females. There was no evidence that any system approaching the "harem" organisation described by Zuckerman for Papio hamadryas could exist on Lolui.

The failure of the "social dominance" concept at a descriptive level has been found in several other recent studies, as described in the introductory section. Kummer and Kurt (1963) stated that in P.hamadryas the criteria of "social dominance" were such that hierarchies within age and sex classes only were possible. DeVore (1965) also found the concept not satisfactory for the complete description of the social behaviour of adult male baboons, and constructed the concept of "central hierarchy" to attempt to explain some of the anomolies and differences.

It seems that the social structure of primate groups under normal conditions probably has little to do with social hierarchies, and the attempts to use this behaviour as a mechanism of social integration is to concentrate on factors which are incidental and peripheral to the basic social organisation.

There is internal evidence from the captive studies of primate social behaviour that the groups under observation were under considerable social stress from a variety of factors, one of the main ones being overcrowding. Other studies of "social dominance" have used different species and genera of primates. Still others have used inadequate experimental designs and criteria.

The primates that are usually used in laboratory and captive studies are in general those which are easiest to obtain and to maintain, adapting easily to the conditions of captivity. The species used are therefore usually widespread savanna or forest-fringe species such as the macaques. It seems likely that these species, including C.aethiops are capable of social adjustment under conditions of ecological deprivation. In the wild this probably results in adult males, already less attached to the group than other age-sex groups, gradually moving further and further away from the group in the day ranges. It is also possible that they might be driven out. The end result will be that the sex ratio of groups under such conditions will be lower than that in non-impoverished areas. There is field evidence of this difference in sex ratio. The increased aggression under captive conditions and the increase in both the frequency and predictability of inter-adult male interactions would seem to indicate that social adjustment to the impoverished conditions of captivity is in process.

These findings and hypotheses emphasise the importance of obtaining reliable and complete information about the relationship of any primate population with the environment in which it is living. Many of the social patterns may only be explicable in terms of this relationship.

Observations on the C.aethiops population of Lolui Island were begun on 23rd April, 1963, and periodic observation periods were continued through until May 23rd 1964. These observations were supplemented by other studies during this time, and by a later one at Chobi in northern Uganda between 24th June 1964 and 17th July.

The majority of the published literature on this species consists of incidental and anecdotal material from hunters or travellers. Information about the basic biology of the species is still comparatively rare. The majority of accounts however, especially those prior to this century, agree that the species is completely arboreal, emphasising the ease with which the species uses trees.

The taxonomy of the entire Cercopithecus genus is confused.

Evidence is presented to show that many of the subspecies and races formerly recognised on the basis of pelage colour are of doubtful validity. Evidence is given that cranial factors do not permit the division of the subspecies C.a.pygerythrus into races. In this study it is proposed to recognise the species group Cercopithecus aethiops, to which are assumed to belong five subspecies, of which the Chobi population is classifiable as C.a.tantalus Ogilby, and that of Lolui C.a.pygerythrus, Cuvier.

The species groups is widely distributed throughout Africa wherever there is savanna or riverine strip vegetation it also inhabits certain forests, but is absent from the Congo Basin, and from arid areas where there is insufficient standing or running water to permit riverine vegetation.

Anatomical evidence is also presented to indicate that the species group is adapted for life in a variable environment. The species group is capable of moving on the ground or in trees and appears equally at home in both. Chromosome studies indicate that this condition is unlikely to be primitive, and indicate that other members of the Cercopithecus genus, such as C.mitis are probably nearer the ancestral condition than are the vervets.

The precise duration of the isolation of Lolui Island from the mainland is a problem to which as yet there is no definitive answer. But it does not seem that it has been sufficiently long, nor the island sufficiently remote, for further speciation to have taken place since the time of isolation. No living specimens found on the island came outside the normal range of variation of the species.

Archaeological evidence indicates two distinct periods of habitation, during the Middle Stone Age, when contact with the mainland was apparently easy, indicating a possible land bridge, and secondly during the Iron Age. The devolution of pottery types found indicates a period of cultural isolation during this time, and the extensive earth works and grinding holes confirm that the island must have been largely self-sufficient for a considerable period; the high level of cultivation resulting in the removal of the forest cover for purposes of cultivation. This state of affairs presumably lasted until the late nineteenth century, when contact with the mainland increased. Then in 1908 the entire human population was evacuated due to the ravages of trypanosomiasis, and the extensive farmlands were left fallow and suitable for ecological succession and finally for reforestation. The old farmlands are now extensive grasslands, and the reforestation is proceeding from the relic and fringe forest patches out into the grassland. The form, structure and the rate of reforestation are all directly dependent on the feeding and day-ranging habits of the monkeys, emphasising the close relationship between the environment and the behaviour of the species, but also showing that the effect is not unilateral.

There is very little competition with the vervets of Lolui Island, the only other large biomass is that of the hippopotamus population, which feeds entirely on grass, and generally not on those species eaten by the monkey population. There are also no predators on the monkeys. This protected position has allowed them to increase, and the population density is very high.

During the day range, the monkeys tend to come out into the grassland. They tend to sit on anthills and termite mounds, and much defaecation and urination takes place here. The faeces are very rich in seeds of the monkey foods, and the locations where they are deposited are ecologically favourable, in that they afford protection from fire, and in the case of the termitaria, better drainage and soil which is brought to the surface through the layer of quartzite sand and gravel that covers it. Saplings soon appear, and the characteristic shape of a vegetation thicket soon appears. The thickets are joined together by Saba florida which extends out into the grassland, and the forest cover is renewed.

This process ensures that rather small areas of forest are extremely rich in monkey food species, and as the reforestation depends on the feeding habits of the monkeys, it is not surprising that the composition of the thickets should include a relatively high proportion of relatively few species. This rich environment has several important effects on the monkey population. It permits a very high population density. It has encouraged a very marked territorial behaviour, with territories that are very small, well defined and vigorously defended. The group distribution patterns at different times of the year depend on the food distribution. In short, many of the characteristic behaviours of this population are the direct result of the particular ecological conditions of Lolui. It also happens that the particular ecological conditions of Lolui are also to a large extend dependent on the presence and behaviour of the monkey population.

Although Lolui is only some six miles south of the equator, there were marked differences in the types of food eaten at different times of the year.Somespecies, such as Saba florida, had a discrete flowering and fruiting season, which in this case was a long season but which was synchronised with climatic factors. Other species, such as Canarium schweinfurthii went through a clear cycle, but were apparently not synchronised with one another. Thus one of these trees might be in fruit, whilst another at the other end of the territory would be dormant having shed all its leaves. Other food supplies, such as burnt insects are dependent on grass fires, the position of which is largely fortuitous, and dependent also on climatic factors. The variations observed at Lolui were sufficient to affect the distribution of the group in the territory. Thus at the onset of the season of heavier rains, little food that was neither fruit nor foliage, such as insects, was eaten. This food was more or less continuously distributed throughout the environment, compared with the discrete distribution of insects, fungus etc., and resulted in a less marked dispersion of the group within its territory. This decreased dispersion occurred just prior to the onset of the birth season, so that when the births began, the group was fairly compact, so offering maximum protection to mother and infants.

Sleeping always occurred within the territorial boundaries in thickets or fringe forest, and generally in the neighbourhood of a high canopy tree such as Canarium schweinfurthii or Maesopsis eminii, although the crown was rarely used for sleeping. There was an observed tendency for groups not to sleep in the same place within the territory on successive occasions. Group 1 had three main sleeping areas and tended to move between them.

Investigative and alarm reactions are described, and the social roles of the different age-sex classes listed. A tendency for infant twos to be interested in the human observer was replaced in the juvenile male by an observed hypersensitivity to his approach. This age-sex group gave significantly more alarms to non-dangerous intruders than did other age-sex classes. The number of juvenile males in a group determined to a large extent the reaction of the group to the observer. As there was a high correlation between the size of groups and the numbers of juvenile males in the group, it followed that the larger groups were those which were more difficult to approach closely. This gives a possible indication of the adaptive significance of larger groups in ecologically impoverished areas.

The social role differentiation of adult males meant that they were particularly involved in vigilance behaviour of the "looking-out" variety, and in the defence of the group against intruders. Looking out behaviour was generally performed by only one or two animals during the day ranging. An individual that had paused from feeding would climb to the top of a tree and sit, in a relaxed sitting position, looking out. It seemed that the appearance of another animal coming to take part in the same behaviour was generally sufficient stimulus for the one already engaged in it to descend and carry on with the normal business of feeding. There was no evidence of any more systematic behaviour than this. The duration of each look-out period tended to be about half an hour.

The main locomotory and social postures are described. The important role played by olfaction in the day to day behaviour of the group is also mentioned. It was not found possible to correlate sitting postures with social status in the way which Hinde and Rowell (1962) did with rhesus. It was thought that certain postures are indicative of the motivational or physical state of the animal, such as "miserable and unwell", and these may well occur as the result of persecution that occurs under captive conditions.

The sexual cycle and sexual behaviour are described. The main forms of friendly behaviour are also listed. An analysis of social grooming indicated that where opposite sex dyads were involved, initiation, by presenting for grooming was almost exclusively performed by the males. Self grooming tended to occur in a peak at the beginning of the day, whereas the peak of special grooming occurred in the evening.

In an analysis of the patterns of aggression it was found that all age-sex classes were equally likely to be involved in aggression, but there were significant differences with regard to aggressors and victims. Adult males were much more frequently the victims of aggression than other age-sex classes. In an experiment on artificial feeding the same equal involvement in aggression was noted, but here adult males were not chased more frequently, which indicates both the lack of privilege or priority of access to a preferred food object - the degree of desirability of the food is indicated by the fact that the rate of aggression increased by over seven times at the pile of nuts. Secondly, the experiment suggests that the chasing of males normally observed during the day-to-daybehaviour of groups is not fighting over food, but originates from other social causes.

Maternal behaviour is described, and the changes in this behaviour associated with the maturation of the infant are also detailed. The changes in contact with the infant, and "aunt" behaviour and the possible adaptive significance are discussed. The norms of social development of infants are described as far as possible, and the development and decline of social play is also documented.

Finally, territorial behaviour is described. The scent marking of territorial boundaries by both males and females is described in detail. The stability of boundaries and the different types of territorial dispute and their causes are also described in detail. The defence of the group, the chasing out of intruders, is apparently the role of adult males. It was only in this context that adult males were observed in close proximity, and co-operating in aggression against another individual. This pattern is very different from the social patterns within the group and emphasises the differences in social role which occur within the group, and which the individual must learn by the time it becomes an adult. But, it must be emphasised, it is not only adults that are "useful" to the group, the important role of juvenile males has been described.

The normal patterns of social organisation and behaviour to be found within this population of C.aethiops are only comprehensible in terms of adaptation for the particular ecological conditions of Lolui. To attempt to describe the social structure in terms of an inadequate "hierarchy" theory leads to distortions and errors in data collection and interpretation. It is an oversimplification and a model which carried with it unjustifiable motivational overtones, and can with advantage be discarded.

APPENDIX 1.

Reference numbers of the British Museum collection of skins of Cercopithecus aethiops.

A. *Cercopithecus pygerythrus pygerythrus.*

No. in Table 1	British Museum No.
1	22
2	169
3	p.6
4	21.1.18.1.
5	159

B. *Cercopithecus pygerythrus rufoviridis*

No. in Table 2	British Museum No.
1	1936
2	1842
3	K/3
4	no data
5	8391
6	no data
7	K/2
8	10
9	211
10	0.11
11	19.1
12	10524
13	2003
14	83.2.6.1.
15	1819
16	1917
17	1880

C. *Cercopithecus pygerythrus johnstoni*

No. in Table 3	British Museum No.
1	1053
2	3/66
3	6875
4	161
5	52.1547
6	no data
7	20
8	79
9	3/59

APPENDIX 2

The population of C.aethiops at Chobi.

Chobi is located on the north bank of the Nile $32^{\circ}10'E$, in an area of savanna woodland that is characterised by a high density of Terminalia glaucescens. The actual banks of the Nile, however, carry a vegetation that is dependent on the presence of the river and which has affinities with the climatically wetter areas of Uganda.

Terminalia glaucescens savanna woodland is the tallest vegetation community and is found at varying distances from the Nile, from a few hundred yards to three miles away, depending on the degree of damage done by elephant. T.glacuscens is very susceptible to elephant damage and does not appear to regenerate when barked or pushed over.

The grass cover is tall and tufted and is a complex of Hyparrhenia filipendula, H.rufa, H.variabilis with Setaria sphacelata, Brachiaria decumbens, Panicum maximum, Chloris gayana, Paspalum commersonii and Cynodon dactylon.

Near the Nile there are considerable stands of Acacia sieberiana with the same grass cover as the Terminalia woodland. On the much broken and eroded banks of the Nile is a relic community which is a thinned out riverine vegetation with Chlorophora excelsa, Spathodea campanulata, Albizia sp. Markhamia platycalyx, Ficus spp., Phoenix reclinata, Alchornea cordifolia and Phyllanthus discoideus.

The trees are often badly damaged and there is colonisation by Securinega virosa and Hoslundia opposita with the spiny climber

Capparis lilacina and *Ipomoea cairica.* There are some grasses which are closely grazed such as *Cynodon dactylon* and *Brachiaria decumbens* and in the less accessible erosion gullies dense stands of the reedy *Panicum deustum.*

The variations in the vegetation seen at Chobi are brought about by the grazing pressure of the many game animals. The principal diet component of elephant is grass and herbs but they also cause considerable damage to tree species which react in different ways. *Terminalia glaucescens*, a main diet component of *C. aethiops*, is very susceptible to elephant damage and dies when barked; it is also easily uprooted. Large areas of the Murchison Falls National Park which were once dominated by this tree are now treeless *Hyparrhenia* grassland.

Combretum gueinzii and *C. binderanum* are broken down by elephant and give rise to a regrowth form which can be described as elephant coppice which is fairly leafy and survives if not overgrazed.

Several species other than elephant and including giraffe feed on the coppice regrowth vegetation and it appears that at high levels of exploitation the coppice growth is eventually supressed. This leads to the apparent elimination of tree species from the grassland. In fact careful transecting in grassland revealsthe presence of numerous very supressed shoots of all major tree species found in the *Terminalia* and *Acacia* savanna woodlands. This geophytic survival of tree species is characteristic of the Murchison Park grasslands (Bueckner & Dawkins, 1961). Certain tree species are less damaged by animals, and *Kigelia*, *Phyllanthus*, *Oncoba*, *Vitex* and *Gardenia erubescens* survive as trees, although young individuals become supressed when grazing pressure is high.

Hippopotamus, of which there are very many, are grazing animals exerting a great pressure on the grasslands near the river and up to a distance of four or five miles away. The extent and pressure of their grazing is largely responsible for the grass communities found at Chobi. Nearest the river there is complete annihilation of the grass cover with consequent sheet erosion. Where any grasses survive it is generally *Cynodon dactylon*, especially near the termitaria. Inland of the eroded areas grazing pressure has converted the grassland to a tufted low ground cover community dominated by *Sproobolus pyramidalis* which extends as far as the *Terminalia* woodland and merges with the grasslands normally associated with that species. Rhinoceros eat fruits of various trees, especially *Kigelia aethiopica* and *Acacia sieberiana*. Because of the dunging habits of this species, with faeces often deposited in the same spot on successive nights, concentrations of seedling and sapling trees of this species often occur there.

C.aethiops and *Papio doguera*, which both occur at Chobi and which are in direct competition with one another feed from several tree and shrub species. On the Nile banks these are mainly *Ficus*. spp., *Hoslundia opposita* *Securinega virosa*, *Capparis lilacina*, *Phyllanthus discoideus*, *Alchornea cordifolia*, *Phoenix reclinata* and *Chlorophora excelsa*.

In the savanna woodlands occur *Acacia sieberiana*, *Gymnosporia senegalensis* *Bridelia sclevoneura*, *Piliostigma thonningii*, *Annona* senegalensis, Securinega virosa, Phyllanthus discoideus and Vitex fisheri. Many of these latter species are now at a considerable distance from the river across the Sproobolus pyramidalis grassland, or exist as geophytic survivors without fruits. Acacia sieberiana is still found close to the river and is a basic food of both vervets and baboons.

The Chobi habitat is therefore very different from conditions at Lolui; whereas the latter is rich and regenerating, the former is an impoverished and deteriorating habitat, due mainly to overgrazing by large mammalian species. The vervet population is also in direct competition with the baboon population.

120 observation hours of the Chobi population were completed between 24th June 1964 and 17th July 1964. The study was concentrated on three groups (Fig. 9) the sizes of which were 25, 13 and 16. The population density at Chobi was approximately 57 per square mile, compared with 225 per square mile on Lolui. The core areas of the groups were located along the narrow strip of riverine vegetation. The groups always slept in these trees, and spent some time during the day foraging there, gradually moving out into the grassland and the Acacia and Terminalia woodlands. The nature and availability of food in the grasslands at Chobi ensures that groups in grassland must be more dispersed than is the case at Lolui. The dispersal indices for Group 1, Lolui Island in June 1963 was 95 and in August 117. The data for Chobi, obtained in the same manner by drawing a contour ring on a sketch map round 75% or more of the group gave a mean value, for grassland ranges and dispersion in Acacia and Terminalia woods of 357. The maximum dispersion observed was 464.

In grassland walking a very characteristic behaviour pattern was observed that did not occur on Lolui. Animals beginning to walk through grass, or continuing walking after sitting feeding for some time always took the first few steps with the tail held vertical. This contrasted strongly with the normal position of the tail in grass walking on Lolui, where it was normally held horizontal. Starck and Frick (1958) also record the vertical tail position in grassland running in their Ethiopian population. The function of this behaviour, which is necessitated at Chobi by the long grass and group dispersion is to give information on the position of a group member moving position to other members of the group.

No territorial behaviour was observed in the Chobi population, no scent marking or jumping round, and no chasing out of "intruder" groups. There was in fact an amount of overlap between two of the groups, the area involved being shown in Fig. 9. Overlap between the other groups, or indeed contact between them was not possible because of the presence of the Chobi river which represented an impassable barrier. Inter-group grooming between the two groups which could interact (Groups 1 and 2) was observed on five occasions.

It was not possible to state definitely whether there was a birth season at Chobi, and no infant ones were observed there. The ages of the infant twos were such that a restricted birth season could not be ruled out, and did in fact probably occur there. The bond between mothers and infants seemed particularly strong at Chobi. On many occasions the infant two of any mother, on seeing the mother begin either to groom or be groomed by another animal, would stop whatever it was engaged in and dash up to the mother and attempt to insert itself between the two grooming animals and suckle from the mother. If the infant was allowed to, and they were only infrequently rebuffed, this brought the grooming session to a natural conclusion. Copulation was also once stopped in this manner, by an infant two jumping at a mounted and thrusting male, who descended and moved off, without any threat at the infant. It is likely that a more intense mother-infant bond might be necessary in areas where the group is habitually very dispersed in normal day ranging.

No evidence of predation was seen during the study period, although there were predators such as leopard in the neighbourhood. Interactions with other species were not common, although several play episodes between juvenile vervets and infant-two baboons were observed. The patterns observed were generally grapple-and-bite and chasing behaviour, although an infant baboon attempted on several occasions to mount a juvenile female vervet; he had a penile erection, but did not achieve penetration. Adult male vervets took no notice of infant interactions with baboons, but adult females were seen to threaten the baboons which were playing with the vervets.

The threat and alarm vocalisations and postures were the same as those observed on Lolui, but the vocalisations were much rarer. There was also no alarm reaction to the observer by the population even on first approach, although when discovered in grassland they tended to run back to the riverine vegetation. The area is, of course a National Park, which probably accounts for this difference in behaviour.

There were indications that the greater dispersion of groups necessitated by the ecological conditions of Chobi had resulted in changes in the frequency of social interactions. Whereas 129 incidents of social grooming were observed on Lolui in a single group over a period of 19 days, there were only 58 observed incidents in a single group at Chobi over a period of 22 days. The mean number of aggressive incidents within the group was .18 an hour, although it may well have been higher because the greater dispersion of the groups and the taller grass made visibility even more difficult.

The population at Chobi seems therefore to be less cohesive than on Lolui, although the mother-infant bond seems more intense. The main differences between the two populations are attributable directly to differences in the ecological conditions offered by the two habitat areas.

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