THE SOCIAL BEHAVIOUR AND ECOLOGY OF *INDRI INDRI*

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Adult male *Indri indri* (Gmelin 1788) in the forest of Analamazoatra, Madagascar.

Adult female and infant *Indri* (aged about six months) at Analamazoatra.

TABLE OF CONTENTS

ABSTRACT

A period of 15 months was spent studying the behaviour and ecology of *Indri indri* in the eastern rain-forest of Madagascar. Two groups were habituated to the observer and followed every six weeks for a complete year. Quantitative sampling techniques were developed which allowed several animals' behaviour to be simultaneously recorded.

Surveys were conducted in three areas of different botanical and topographical structure and censuses performed both at the beginning and end of the study. Some behavioural properties of a population of *Indri* were investigated in one study site by collecting data on vocal interactions between approximately 40 groups.

The maintenance activities of the species are described and assessed. Seasonal and individual variation in behaviour are compared both in the groups studied and with other species. Social behaviour is analysed (1) by measures of animal interaction and (2) in terms of the inter-dependence of some individuals' behaviour with others. Measures of spacing and feeding are shown to be suitable to this approach. Evidence for the territoriality of the species is presented and its adaptive qualities considered. The roles of territory definition, declaration and occupation are contrasted and compared. The development of behaviour in infant and juvenile *Indri* is examined in terms of individual and social adaptations.Some facets of ecological and social differentiation with *Indri* society are proposed.

Indri are found to live in nuclear family groups occupying small, defended territories. Most aspects of their behaviour are seen to vary seasonally. Low rates of reproduction and a long maturation period appear to be linked to short daily activity periods and small but stable supplies of food. Like many other lemurs Indri live in a matriarchal society. Female dominance is rarely expressed by interaction, but adult males, and to a lesser extent other individuals, are limited both in their position in trees and their activity. Convergences between family living primates in three widely separated divisions of the order throw light on the evolution of primate social organisation and the social behaviours which mediate it.

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CHAPTER CONTENTS

CHAPTER 5 LOCAL SPACING 145

LIST OF APPENDICES

LIST OF FIGURES

FIGURE

LIST OF TABLES

TABLE

TABLE

TABLE

TABLE

LIST OF PLATES

CHAPTER 1

Introduction

There are two major interpretations of the way primates came to inhabit Madagascar. In one, part of an ancient land mass (Gondwanaland/Laurasia, Du Toit 1937) became unstable and from the Jurassic or Lower Cretaceous (about 120 million years ago) profound activity in the underlying geological structures took place. This led to a 'spreading' of the sea floor and caused the land mass to disintegrate ('continental drift') in movements that can still be measured at the present time (Kurten 1969). At about the time of the initial radiation of the mammals (just before or at the beginnning of the Tertiary era) the island that is now Madagascar became separated from the mainland of Africa[1]. Either local mammalian species were thus isolated on the island as it drifted away from the mainland, or as a more likely explanation, rafts of vegetation - debris that fell into the great East African rivers, such as the Limpopo and Zambesi - carried small mammals across the narrow Mozambique channel enabling them to colonise Madagascar. It is probable that animal invasions occurring in such a manner did not take place for long and eventually ceased as the island moved further from the mainland coast (Simpson 1940, Walker 1972, Martin 1972b), although some authorities consider that invasions of this kind may have occurred at several different points in the island's history (Mahé 1972, Tattersall 1973).

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[1] The original alignment of Madagascar was probably along the coast of Tanzania or Mozambique (Gilbert Smith and Hallam 1970, Walker 1972), although the absence of Palaeozoic rocks such as Table Mountain sandstone and the Waterberg series indicate a more northerly origin (Dixey 1960, Heirtzler & Burroughs 1971).

As a result of 'sweepstake' invasions, it is probable that the mammalian population of Madagascar in the early Tertiary largely consisted of small, primitive forms with few competitors or predators. The rapid radiation from this basal mammal stock that followed, filled many of the vacant ecological niches - an adaptive evolution that was independent of but in many ways mirrored that occurring in Africa at the same time. The main difference between early mammalian evolution in Africa and Madagascar concerned the variety of the basal stock which in the former far exceeded the latter.

Primitive primates formed the main stem of mammalian evolution on the island of Madagascar and species developed of great size (e.g. Megaladapidae) perhaps taking the role of browsing, forest-living ungulates, specialised insectivores (such as the aberrant, Daubentoniidae) and baboon-like omnivores (such as Hadropithecus and Archeolemur), in addition to a variety of smaller, partially insectivorous, fruit and leaf-eating forms.

The arrival of man on the island from sources as diverse as South-East Asia, India and Africa ensured that the primates of Madagascar received, from the first few centuries A.D., a powerful competitor (Battistini & Verin 1967, 1972, Walker 1967, Mahé 1972). It was probably competition for resources - mainly the great forests covering most of the island - that accounted for the extermination of about 50% of mostly the large-bodied primate species, although some authorities claim that man was only an observer of forest destruction resulting from climate changes (Lamberton 1934). Today 20 species of primate remain in Madagascar (the Malagasy lemurs), but at least 6 of these are in immediate danger of extinction.

An alternative interpretation, favoured by the Betsimisaraka people (a tribe inhabiting the northern half of the east coast of Madagascar) places a closer relationship between all primates, including man, than would be supposed from the scientific view exposed above. In one of many similar, popular tales of folklore the evolution of the lemurs is traced from two god-like characters,

> "Jaobinohoka and Ranaivotovoana who convened one day in order to create human beings. It was decided that Ranaivotovoana would make their bones and flesh and Jaobinohoka would add the blood and the 'life'. Beginning their project Ranaivotovoana cut down a tree and carved out two human figurines, adding the final touches in clay. Jaobinohoka meanwhile made blood from water and filled up the figurines with it. Having bestowed life upon them, the two effigies became human beings - one male and the other female. They were named "Monka", which means man.
>
> The two humans had children which themselves reproduced and soon a great population arose. Divisions and tension resulted in wars between two rival factions and eventually one of these emerged the winner, remaining men, whilst the losers fled to

the forests and became lemurs. This explains why lemurs have fingers like those of men and when they cry they recall their ancient origins, calling "Monka! Monka!". "

The many legends on this subject all imply a derivation of lemurs from man rather than vice versa, and although aggression is the usual cause of their original division most of the tales put a more affiliative emphasis (often describing episodes of mutual aid or saviour-benefactor) on their relationship.

Whichever interpretation best serves the scientist studying the Malagasy lemurs, it is without doubt the second which has contributed most at present to their protection and conservation, through the action of (sometimes powerful) taboos prohibiting their killing or consumption. Although widespread, especially amongst the rarer species of lemur, taboos in Madagascar have not balanced the effects of forest destruction on lemur populations. A unique and diverse complement of animals and plants on Madagascar has evolved on 'continental' lines, in many ways paralleling their separate evolution in Africa, Asia, Europe and America. The independent adaptation of the Malagasy flora and fauna has remained until recently largely unstudied (Battistini & Richard-Vindard 1972, Martin et al 1974, Tattersall & Sussman 1975a) despite the praise-worthy efforts of the French overseas institutes (O.R.S.T.O.M.).

1. THE AIMS OF THE STUDY

1.1. General aims.

Two classifications of primate society have been recently proposed (Crook & Gartlan 1966, Eisenberg et al 1972), stimulating widespread discussions about the nature of the evolution of social behaviour in the order. Both the classifications trace or imply an evolutionary trend of increasing group size which is influenced by environmental variability to limit precise allocations of all species to particular socio-ecological grades. These useful attempts to integrate studies of primate social behaviour and ecology into a testable hypothesis of socio-ecological adaptation have suffered justifiable criticism from several different angles:-

(1) the allocation of particular species to particular divisions of the classification (Richard 1973)

(2) the variability of group size within the same environment and species (Clutton-Brock 1974b)

(3) similarity of the size and structure of social groupings within taxa in different environments (Struhsaker 1969, Rowell and Chalmers 1970)

(4) the omission of consideration of reproductive parameters (Goss-Custard et al 1972)

(5) the dependence on 'blanket terminology' in classifying primate habitats as 'forest', 'woodland savannah' etc., and primate diets as 'folivore', 'frugivore', 'insectivore' etc. (Richard 1973).

Objections to an imprisoning allocation of species to defined socio-ecological divisions are being voiced as it is becomes evident that the effects of the environment on social organisation appear to differ according to a species' phylogenetic history. As this means that the influences of phylogeny and environment can not be separated a priori it is essential to consider evolutionary changes in social organisation rather than attempt a direct extrapolation from extant forms. This approach may be pursued in two ways: one may apply a behavioural approach which involves the elucidation of the social characteristics of extinct forms from anatomical data; and one may apply an ecological approach by examining the probable nature of ancestral environments (see, for example, Robinson 1973) and retrospectively fitting species and their social organisations into them using socio-ecological 'rules' obtained from studies on extant forms. The behavioural approach concerns, in practice, the description of the social organisation of those primates for which there is evidence of retention of a high proportion of ancestral characteristics such as the Galaginae and Cheirogaleinae (Charles-Dominique and Martin 1970) and other prosimians.

Crook and Gartlan's (1966) distribution of primates to adaptive 'grades' (Table 1.1) placed the prosimians firmly on the 'primitive' side of the classification - primarily because they lived in smaller groupings (maximum size 30) than many simian species (maximum size several

TABLE 1.1. Adaptive grades of primates (from Crook & Gartlan 1966).

hundreds). An alternative approach is to regard group size in the Lemuroidea (which contain the greatest variety of prosimian social organisations - Petter 1962) to be limited for phylogenetic reasons, and thereafter consider variation to be dependent upon the environment. This attitude recognises that the Malagasy primates have been genetically isolated from those in Africa/Asia for at least 60 million years and socio-ecological adaptation within the island (which possesses a sufficient variety of habitats) may mirror that which occurred elsewhere. Similarities in the type of social organisation of primates living in comparable habitats in Africa/Asia as those in Madagascar, for example, would offer convincing associations between social organisation and environment which would be virtually independent of phylogeny. A similar reasoning can be applied to other mammalian orders and encouraged Barash (1974) to make a study of comparative socio-ecology within one sciurid genus (Marmota) with profitable results.

Studies of the social organisation of a primate group require observation of all the constituent relationships and the forms of communication which mediate them. If possible, this should be followed by an examination of functional considerations of the effect these relationships have on individuals' survival and reproductive capabilities. Ideally, the behaviour of all group members should be recorded all the time so that the effect of each individual's behaviour on every other member of the group can be examined. The lemurs of Madagascar are well suited to this approach because:

(1) group size is small and dispersion of group members usually limited to viewable distances

(2) the frequency with which their behaviour changes is low (Petter 1962, Jolly 1966)

(3) the variety and frequency of social behaviour is often low (Petter 1962, Jolly 1966, Richard 1973). The retention of the rhinarium in lemurs and lorises ('Strepsirhines' Hill 1953) probably excludes fine movements of the facial musculature and facial expressions are either rare (Andrew 1963) or quite absent (pers. obs.). Furthermore, vocalisations are generally discrete rather than graded (Andrew 1963, Marler 1965).

1.2. Specific aims.

The 'indris' or 'endrina' (Indri indri - Gmelin 1788) was first discovered by Sonnerat in 1780. Reports of this large, tailless lemur living in small groups of 2-8 individuals in the eastern rain forests of Madagascar (Milne-Edwards & Grandidier 1875, Rand 1935, Petter 1962) suggested that this species would be suitable for a detailed study of social organisation with the aims and in the manner described above. Additional reasons for the choice of this species were:

(1) Study of a lemur inhabiting a rain forest environment was required to compare with previous research on species living in the west or south (Jolly 1966;

Richard 1973, 1974a, 1974b; Sussman 1972, 1974, 1975; Harrington 1971, 1975, Martin 1972a, 1974). As no rain forest living species had been intensively studied in the past, information was required on lemur ecology in this substantially different environment so that the full range and diversity of their behaviour could be appreciated. More specifically, a precise, long-term study on Propithecus verreauxi had been made in the dry, seasonal forests of the north-west and south of the island. Comparing the relationship between behaviour and ecology in Propithecus with that in Indri, a member of the same taxonomic family (Indriidae) living in a very different environment, would permit interesting associations to be made between lemurs' habits and their habitats.

(2) Claims by Petter (1962) that Indri lived in groupings similar in composition to those of Propithecus offered the possibility of making two comparisons of interest:

(a) studies of Indri living in 'extreme'(smallest and largest) group sizes to examine the consequencies of the 2 situations for individuals' feeding, ranging and defence strategies. Clues may be obtained from this approach to the effect of group size variation on group members' behaviour.

(b) the genetic relationship between individuals in groups of different size may vary extensively if some groups are truly nuclear family units (Petter 1962) whilst others contain, in addition, unrelated or more distantly related individuals. The type of social interaction between individuals in such groups may depend on their "inclusive fitness" (Hamilton 1971) - the amount of effort (energy and time) expended on bringing their offspring to reproductive age (Orians 1969, Trivers 1972). One might predict that the relatedness of individuals would influence their social relationships, and species living in family groups and larger groups could be profitably examined to investigate this possibility.

2. THE STUDY SPECIES

Indri indri (Frontispiece), the largest living lemur, inhabits central and northern parts of the Malagasy rain forests. Indri indri is an arboreal 'vertical clinging and leaping' lemur (Napier and Walker 1967) and lives in the dense forests lining the east coast. Further inland, its distribution extends westwards to regions 1500-1800 metres above sea level. Indri are found as far north as Maroansetra and the southern limit to their distribution appears to be the River Masoro (see Figure 2.1). Although specimens have been collected in the past from Sambava, Indri no longer inhabit this area (Peyrieras pers. comm.). The species is confined within this distribution (Fig.2.1) to wet, evergreen forest where it feeds during the day, on leaves and fruit.

The genus Indri (Cuvier and Geoffroy Saint-Hilaire 1795) contains but a single species. The morphology of Indri has been comprehensively described by Milne-Edwards and Grandidier (1875) and Hill (1953) and is found to differ from Propithecus chiefly in general size, by its vestigial tail stump (unique in living lemurs), in the presence of a laryngeal air sac, its large external ears, and the thick silky fur.

Indri are not sexually dimorphic in size or colouration. The fur is mainly black or white or various shades of grey and the colours are distributed in a pattern that is consistent between individuals. Within the pattern, however, the relative brightness of colouration varies extensively - some animals having pure white and black fur, others varying in shades of grey or black. A triangular shaped lightening of the pelage (often absolutely white), its base at the 'tail' and its apex in the middle of the back, is typical. A bright white or greyish patch of fur in the top of the head which may extend to form a collar around the neck is also very common[1]. The outsides of the arms and legs are often whiter than the insides but the extremities and ears are jet black, the face relatively hairless and quite black. White smudges above the eye (and around the throat) are common, especially in young animals.

Confusion resulting from the extreme variability in pelage colouration (Hill 1953) led some authors to believe that several species existed (Lacépède 1800, Gray 1872) but observations made during this study support Hill's contention that these varieties in pelage are solely of an individual nature. Indri found during the present study

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[1] Hill (1953 p.612) is incorrect in stating that the crown of the head is entirely black. 50% of Indri seen in this study possessed bright, white crowns.

varied as much in pelage colouration within as they did between study areas.

Indri's head plus body length is quoted by Hill (1953) as 700 mm and although no published data on body weight is available this probably lies between 9 and 12 kgs for fully grown adults.

Previous observations on Indri in the wild are few and only anecdotal accounts of their behaviour have been reported. Many authors refer to the loud calls of Indri which are assumed to have a 'territorial' function. The fullest report of Indri behaviour was written by Petter (1962) and recently an account of Indri population density and home-range size has been published by Petter and Peyrieras (1974).

Despite several attempts captive Indri have never been kept alive for long. The Paris Menagerie received 8 or 10 specimens in 1939 but these did not survive one month. At the French research institute, O.R.S.T.O.M., in Tananarive, Indri also died soon after captivity having refused to eat the standard diet of milk, bananas, tomatoes and various other fruits. At the time that the study ended there were no captive Indri in Madagascar or elsewhere in the world.

Indri more than any lemur (with the exception of Daubentonia madagascariensis) is the subject of Betsimisaraka mythology. It is widely believed that Indri are religiously 'protected' and that attempts to kill them will fail (i.e. they are immortal) or will invoke some terrifying reciprocal action. Eating Indri is held to result in paralysis or death. The importance of taboos ('fady') of this nature is probably diminishing as a result of the action of missionaries and from better communication with other (developed) countries. During the period of research reported in the following chapters it is certain that Indri were not captured by local people. Considerable concern was shown by these people when a government agency employed some of them to construct Indri cages[1] in the forest to encourage tourism in the region.

3. THE STUDY IN MADAGASCAR

The research visit to Madagascar lasted from 13th May 1972 to 8th August 1973. Due to a month of political disturbances surrounding a change of government, the beginning of the project was delayed until 12th June 1972. Between this date and the time of departure from the island, observations of rain forest living lemurs were made on 343 days. During this time Indri were studied for approximately 2000 hours. Most of this time was spent in quantitative observations on 2 main study groups (see Chapter 2) but 16 other Indri groups were also watched for a total of about 200 hours.

The study began and ended in the middle of successive austral winters separated by single warm, wet season. Indri were observed equally at all times of the year (see Chapter 2). Other common species living in the region, notably Hapalemur griseus, Lemur fulvus fulvus and

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[1] These cages did not contain any lemurs in early 1975 (McNulty,pers.comm.) as funds for the project had been terminated.

Propithecus diadema diadema, were frequently seen and notes made on their behaviour. Observations were also made on Varecia variegata and Lemur rubriventer, and during the night, Microcebus murinus rufus, Cheirogaleus major, Avahi laniger laniger, and Lepilemur mustelinus. In April 1973 one week was spent in the forest of Ankarafantsika (Ampijoroa) to observe Propithecus verreauxi coquereli in a dry, seasonal forest environment. With this exception and ignoring 2-day visits to the capital, Tananarive, every 6-weeks, each day in Madagascar was spent observing rain forest living lemurs.

4. ORGANISATION OF THE THESIS

No information presented in this thesis is treated as evidence for any specific taxonomic division within the primate order. The theme of the thesis is one of descriptive natural history and, to avoid controversial issues, the classification of Simpson (1945) is adhered to. It has been found useful to include, when distinguishing attributes of lemurs (including Daubentonia) and lorises from other primates, the respective terms 'strepsirhine' and 'haplorhine' in the sense used by Hill (1953 et seq.).

Following a description of the study programme and the observational problems encountered (Chapter 2), the type of information recorded during the study and methods used in its analysis are presented (Chapter 3). The composition of groups of Indri and measures of population density (Chapter 4) are followed by a quantitative analysis of spacing within the two main study groups (Chapter 5). Descriptive Chapters 6, 7 and 8 on Feeding, Ranging and Social Behaviour follow. Measures of "Feeding Behaviour" are not restricted to Chapter 6, as the activity was found to be of importance in examining several different attributes of social relationships. The relationships between different groups of Indri are investigated in Chapter 9 and a descriptive account of major features of infant development (Chapter 10) completes the presentation of data.

During the course of the thesis certain terms are employed which may be ambiguous, through controversy surrounding their usage or by inexact application of their normal meaning:

(1) "Seasonality" or "seasonal variation". Variation in individual or group behaviour between periods of observation (which occurred at intervals of about 6 weeks) is termed "seasonal variation". This is not meant to imply that such variation would be consistently found at the same time of each year but is used as a description of variation that occurred throughout the year's observations. Where differences between climatic seasons are involved the names of the seasons themselves are employed.

(2) Indri were found to live in defended, exclusive and probably permanent territories surrounded by a small area of 'common land'. The definition and importance of territorial life to Indri is not discussed until Chapter 9 and the term "home-range" is used to denote the region

through which Indri groups moved during the year (see Chapter 7).

(3) The "availability of food" to animals is used below to include knowledge of the location of food as well as its physical presence and the means to eat it. In this sense, therefore, food is not available to animals unless they are aware of its existence and are able to obtain it.

CHAPTER 2

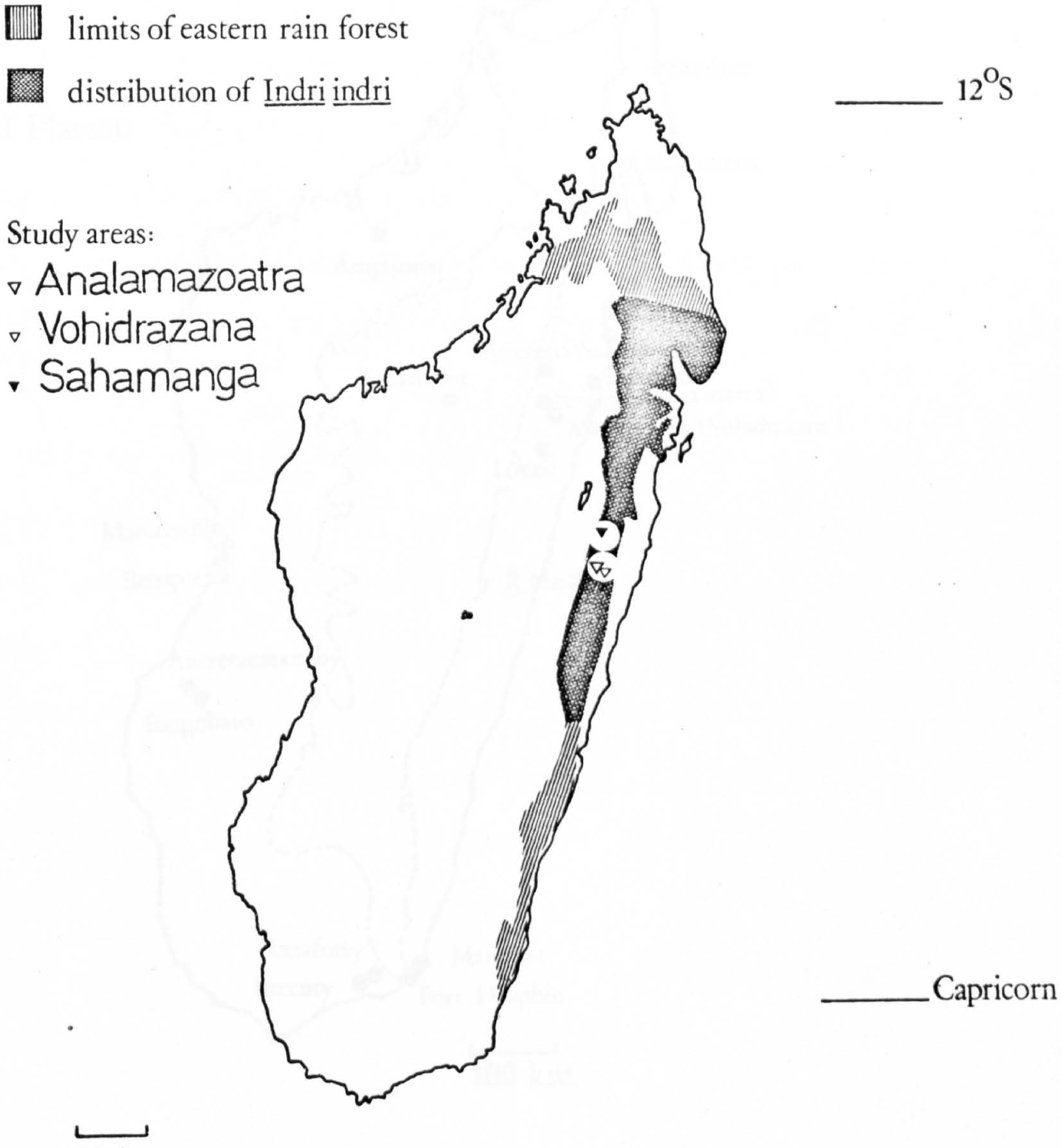
Animal Observations and the Nature of the Information

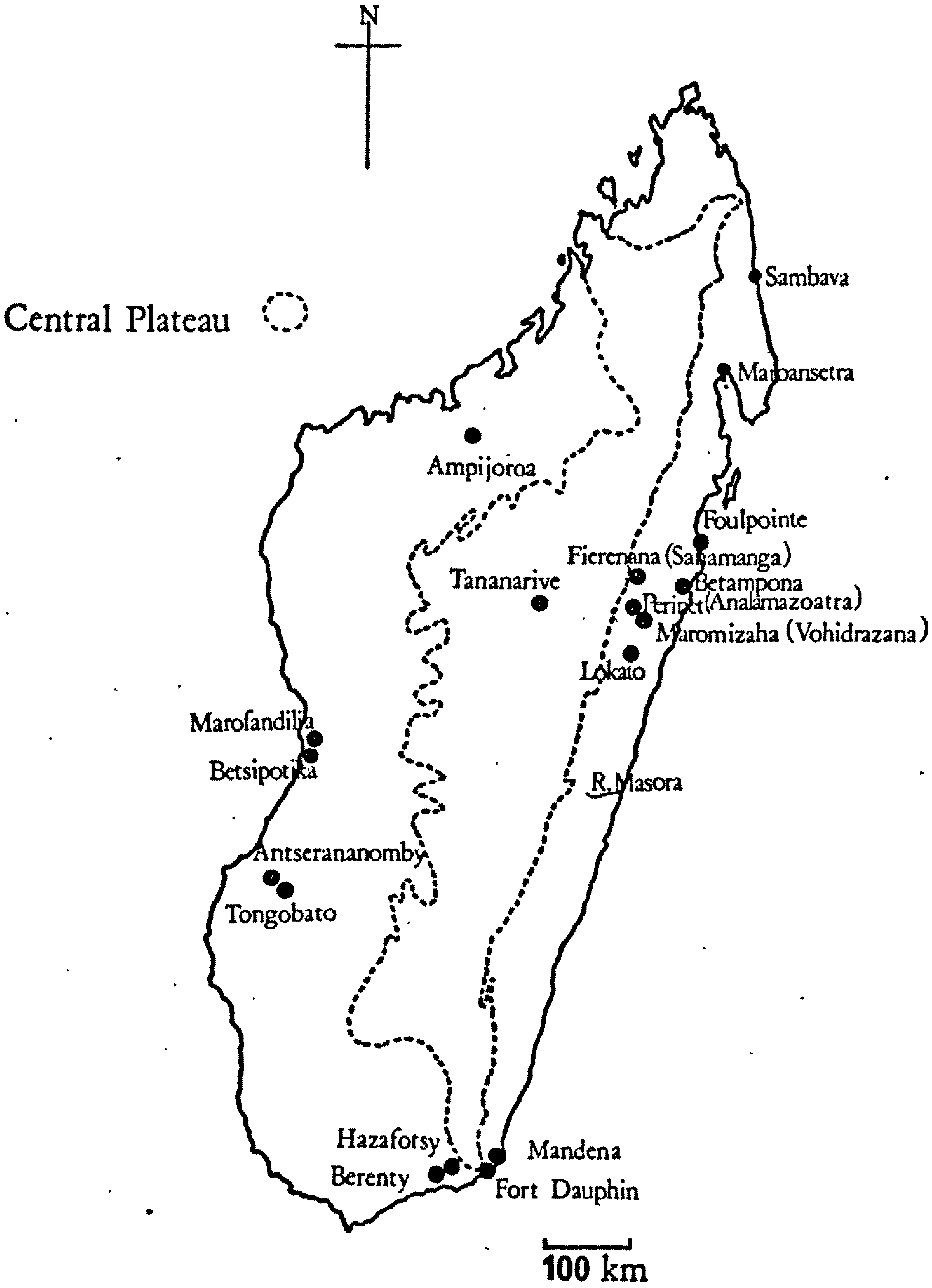
The original aim of the study - a direct look at the social consequences of variation in group composition in a rain-forest lemur - was based on published reports of Indri living solitarily or in groups of 2 to 8 individuals. It was primarily intended to study feeding, ranging and social behaviour in a number of groups of different size and attempt to correlate aspects of individual and group behaviour with several parameters of the social environment. Thus measured variation in feeding activities, for example, might be directly attributable to facilitation of food location afforded by group members. Animals living in different groups, it was thought, might have to pursue different strategies of food attainment if too few fellow members were present.

1. STUDY METHODS

A period of 4 weeks was initially spent in the forest of Analamazoatra (see Fig. 2.1) investigating the feasibility of the study. A group of Indri were habituated and followed daily to examine suitable methods of data collection. Due to the degraded nature of the forest and widespread human habitation attempts were then made to find some isolated primary forest lacking human interference. It was already clear at this time that the species under study lived only in aggregations of 2 to 5 individuals and this was confirmed by extensive questioning of local people.

Figure 2.1 Maps of Madagascar showing the probable distribution of *Indri indri*, and the location of study areas and places mentioned in the text.


▥ limits of eastern rain forest
▩ distribution of Indri indri
Study areas:
▿ Analamazoatra
▿ Vohidrazana
▾ Sahamanga
12°S
Capricorn
100 kms


N
Central Plateau
Sambava
Maroansetra
Ampijoroa
Foulpointe
Fierenana (Sahamanga)
Betampona
Tananarive
Perinet (Analamazoatra)
Maromizaha (Vohidrazana)
Lokato
Marofandilia
Betsipotika
R. Masora
Antserananomby
Tongobato
Hazafotsy
Berenty
Mandena
Fort Dauphin
100 km

A survey of the forest in the Réserve Naturelle No. 1 at Betampona near Tamatave (Fig.2.1) confirmed reports of a far higher mean tree width and height, less undergrowth and adequate protection of the constituent animals. The density of <u>Indri</u> was, however, prohibitively low and locating animals was therefore impossible. A closer examination of the forèst south of Perinet (towards Lokato) and in the forest of Vohidrazana proved that long term detailed observations would suffer from the cyclonic degradation of ridge-tops, angle of the slope (often exceeding 45°), dense slippery undergrowth composed of webs of elevated adventitious roots and lianes, and heavy morning mists.

The western edge of the rain forest strip was then considered and a site chosen in an untouched area 8 kilometres east of Fierenana (Fig. 2.1). A high concentration of not only <u>Indri</u> but all diurnal and nocturnal rain-forest living lemurs inhabited this forest (Sahamanga), 5 kilometres from the nearest human habitation. A hut was built 3 kms inside the forest's western edge.

During a week's preliminary study in this locality 3 <u>Indri</u> groups were found. The presence, in the primary climax vegetation, of an intermediary canopy layer totally obscured the animals from view when they fed in the highest trees and each group was visible for only 10-15% of the time for which the observer maintained contact. This inevitably and considerably biased records of behaviour in favour of low forest level activities: feeding on saplings and earth, defaecation and locomotion, activities normally occupying a small fraction of their time. It was therefore decided that primary forests were not suitable locations for accurately gauging temporal and seasonal distributions, overall proportions and individual variations of Indri behaviours.

By this time it was evident that original ambitions concerning the simultaneous study of numerous groups of different sizes would be impossible to realise as the time spent in locating, following and habituating (see below) new groups proved excessive. The project was modified in aim so as to concentrate on obtaining information on individual behaviour in a few groups for a complete year, whilst regularly visiting other forests in more isolated regions to qualitatively measure gross seasonal changes in lemur activity and make sporadic observations on other species.

2. STUDY AREAS

1. Forest of ANALAMAZOATRA. (Perinet). Latitude $18^{o}56'$, Longitude $48^{o}24'$; Altitude 928 ms. Uncertain of the effects the impending rainy season would have on observation conditions and transport between chosen study areas, a forest with easy access was selected for the required intensive observations. The forest of Analamazoatra consists of a small Reserve administered by the Département des Eaux et Forêts surrounded by experimental plantations of introduced species of Eucalyptus which form part of the programme of research

performed by the Centre Technique Forestier Tropical (CTFT). A set of fish hatchery ponds had been constructed and populated by a variety of species under study. These projects required a certain human population to live in close association with the forest inhabited by Indri, but logging was forbidden and the animals were to a large extent protected.

Additional advantages of this study area were widespread forest tracks (essential for quiet observer movement) and knowledge of the date of birth of one young individual in the selected Indri group. This information provided a useful reference for future age determinations.

As the choice of consumed plant species varied from month to month it was decided to select two study groups in this area and observe each with sufficient frequency to determine their complete repertoire of foods and make crude measures of ranging behaviour. The groups eventually chosen contained (i) extreme complements; 5 and 3 individuals[1], and

(ii) young animals; one aged 2 months, another 14 months, so that the complete 2 year development to sub-adult size could be followed, albeit in different groups,

(Fig. 2.2).

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[1] The group of 3 included a new-born infant.

Figure 2.2 The study area at Analamazoatra showing home range limits of the study groups.

10×8

The forest of Analamazoatra

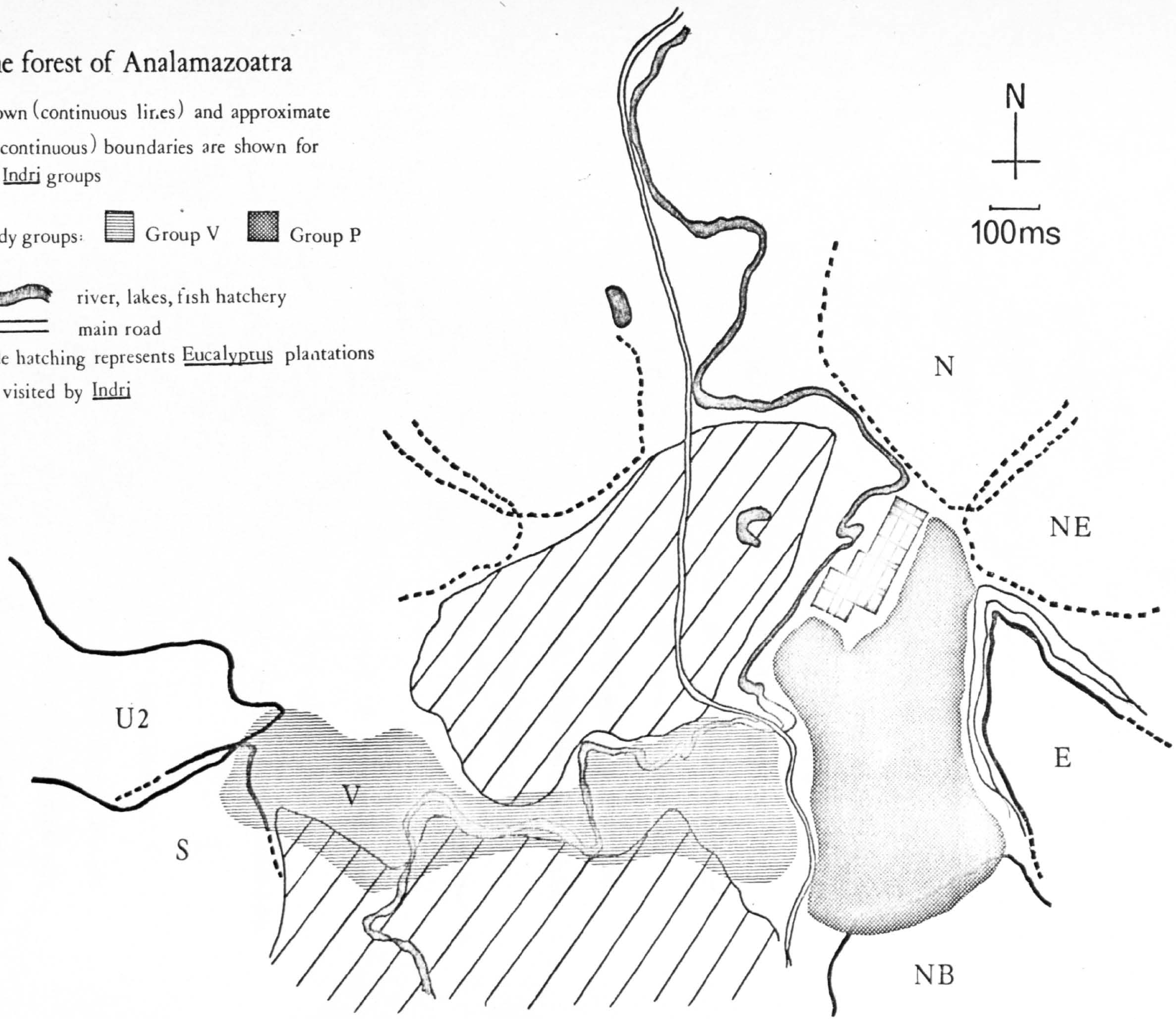
Known (continuous lines) and approximate (discontinuous) boundaries are shown for ten Indri groups

Study groups: ▤ Group V ▩ Group P

river, lakes, fish hatchery

═ main road

Wide hatching represents Eucalyptus plantations not visited by Indri



2. Forest of VOHIDRAZANA. Situated 10 kms. to the east of Analamazoatra at an altitude of 1200 metres, the steep forest in this region was completely free of human habitation and contained high densities of Indri and Propithecus diadema diadema. A fall of earth during a cyclone two years before had cleared a gap in the vegetation exposing to view a large expanse of forest from a single position. From this position the calls of approximately 40 Indri groups could be heard. The vocalisations were attenuated only by the prevailing atmospheric conditions and physical properties of the air, as from their point of origin they travelled through no vegetation (see Chapter 9). Compass bearings could be taken of the source of these calls, their distance estimated, and with practice the groups found. At distances less than 800 metres this method eventually located 70% of the groups within 50 metres of the original estimate of distance in the direction of the compass bearing.

This study area (Maromizaha) was used to record populations of these calls regularly over the year and, eventually, a third Indri group was habituated (see Section 4) in the region.

3. Forest of SAHAMANGA. This study area near Fierenana, located 60 kms. north of Analamazoatra, at an altitude of 1300 + metres, was also regularly visited in order to gauge gross measures of ecological variety in an undisturbed primary forest and make occasional observations on other lemur species: in particular Propithecus diadema diadema, Varecia variegata, Hapalemur griseus, Lemur

fulvus fulvus, *Avahi laniger orientalis*.

By the end of August 1972, intensive study groups had been habituated (see Section 4), the animals were to a large extent immediately recognisable, and their home ranges divided into painted quadrats (see below).

The study was then temporally divided into 8 "Circuits" each lasting 6 weeks from 6 September 1972 to 29 July 1973, each of which was composed of the following schedule:

1st Study Group: 12-14 days
ANALAMAZOATRA
2nd Study Group: 8-10 days
Population vocalisation data: 3 days VOHIDRAZANA
Primary forest observations: 3 days SAHAMANGA
Travel and restock of consummables: 3-5 days
Variable time allocation for observations
in other forests or on other species: 7-13 days

TOTAL 42 days

3. THE HABITAT

3.1. Topography and climate.

The topographical structure of most eastern parts of Madagascar consists of a series of steep crests, running approximately north to south, and budding off successions of secondary folds. These geological 'waves' have amplitudes of up to several hundred feet and lengths of a few hundred to two thousand yards. Towards the coast these folds flatten into the gently undulating low Betsimisaraka hills (Battistini 1972) where the vegetation has been largely destroyed and cultivations of rice and bananas now exist (savoka). The prevailing easterly winds carry moisture to the eastern escarpment which forces them to rise, cool, and deposit up to 5 metres of rain annually on the forested slopes. The rainfall decreases westwards with the rise in altitude which reaches a maximum of 1500 metres 100 kilometres from the coast. A denuded high central plateau separates the western edge of the moist forests from the dry, seasonal vegetation of the western parts of the island, whose annual rainfall rarely exceeds 350 mm and falls only during the summer months.

At Analamazoatra and other study areas, where the ridged structure of the forest contributes to the great variety of atmospheric conditions found between the bottoms of valleys, crest tops and eastern and western slopes, mean annual rainfall varies between 1500-2000 mm, and is distributed unevenly throughout the year (Table 2.1) although mean temperatures vary little between months. The mountainous structure found in most forests is less acute at Analamazoatra which lies only 15 kilometres inside the rain-forest's western limit. Between 1933 and 1964 the absolute minimum and maximum temperatures recorded in Perinet were -5.3° and 33.6°. No detailed records are available from higher forests, but observations in the study area near Fierenana indicated that it was, throughout the year, considerably wetter and colder. In all study areas seasonality in weather conditions was marked - afternoon tropical downpours during the warm austral summer

	J	F	M	A	M	J	J	A	S	O	N	D
Rainfall in mm:	306.0	320.0	261.9	92.4	61.4	76.9	77.8	67.1	51.1	43.9	112.2	237.6
Mean max. temp.:	27.0	27.1	26.1	25.4	23.2	21.3	20.3	20.6	22.2	24.1	26.3	27.1
Mean min. temp.:	16.9	16.6	16.7	15.4	12.9	11.3	10.5	10.3	11.1	12.4	14.7	16.3
Mean temp.:	22.0	21.9	21.4	20.4	18.1	16.3	15.4	15.5	16.7	18.3	20.5	21.7

Overall mean annual rainfall : 1708.2 mm

Overall mean maximum temperature : 24.2

Overall mean minimum temperature : 13.8

Overall mean temperature : 19.0

All temperatures in degrees centigrade. Rainfall data from 1928 to 1960. Temperature data from 1941 to 1960.

TABLE 2.1 Mean monthly rainfall and temperature at Analamazoatra.

(November to March) contrasting with long periods of light rain in other months.

3.2. Vegetation.

The evergreen rain forest flora of Madagascar has been generally but incompletely described by Perrier de la Bathie (1921), Humbert (1936) and Humbert and Cours Darne (1965). A recent treatment of the subject by Koechlin (1972) summarizes contemporary knowledge and lists some of the more common plant genera. The large number of species, their similar physiognomy and the different characters of individual trees of the same species found at different heights on the slopes, make plant description and identification difficult. A small proportion of the floral species are described by Cabanis et al (1970). The few phenological studies made (CTFT, unpublished) illustrate the long periodicity and irregularity of fruiting patterns not only between but also within species (see Chapter 4). Very few, if any, common plants fruit every year.

During the study it became clear that the trends associated with varying altitudes in different forests of the eastern domain were also present on a single mountain. Hence, the wet, mossy, undergrowth-free valleys containing the straightest, tallest trees forming a continuous canopy layer (Fig. 2.1) become gradually replaced by small, densely packed trees, often with twisted shapes and covered with orchids and lichens, near the crests (Fig. 2.2). Exposed rock or huge boulders are common near the valley streams and glades of bamboo are found in thick patches in the

PLATE 2.1 The structure of the forest at the bottom of the valley at Vohidrazana. *Indri* may be seen at the centre of the plate leaping across a gap in the vegetation. Tall, slender trees predominate at these positions.

PLATE 2.2 The structure of the forest (Vohidrazana) at the top of a ridge showing the steep angle of the slope and dense, low vegetation.

higher regions. Tree ferns are common at all altitudes.

The structure of the eastern rain forests is, therefore, locally and regionally heterogeneous and the limited distribution of some plant species, the various gradients of temperature, rainfall and exposure to wind, and the diverse physical organisation of the forest make for a notably complex environment rich in botanical variability.

3.3. Plant identification.

Plants were identified on the spot by a botanist, M. J-P. Abraham, working for the Departement des Eaux et Forets in Tananarive, and later checked against collections housed in the Academie Malgache in Tananarive. Most items consumed on more than one occasion were individually identified. Personal skill in identifying the plant species gradually improved over the course of the study, but in general although family and genus could always be determined, the specific name could not.

4. HABITUATION OF INDRI

At Analamazoatra the two study groups (Group P and Group V)[1] were habituated to the observer by repeated location and following. The adopted method, identical to that used by Richard (1973) for Propithecus verreauxi, met with a very similar response from Indri and varied little between groups. The initial reaction - alarm

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[1] Group P consisted of an adult female, an adult male and three offspring of different ages: O3, O2 and O1 in order of decreasing age.

Group V consisted of an adult female, an adult male and an infant (see Chapter 4).

vocalisations and fleeing - diminished after one week of contact and feeding was occasionally observed before the animals were lost. After 3 weeks animals would approach and feed within a few metres although individual variation in the habituation response was marked, adult females and young becoming precociously tame. The habituation process continued throughout the study and all animals would eventually feed within one foot of the observer (see also Chapter 8).

Habituation of lemurs may result from cumulative as well as sustained contact with humans. Group 4 at Vohidrazana was habituated almost perfectly to the observer over a period of 15 months by 3-day visits every 6 weeks.

Quantitative observations were only begun when all animals would feed within 5 metres of the observer.

5. THE BEHAVIOUR OF THE OBSERVER

5.1. Introduction.

Every field study of primates involves, in the collection and interpretation of recorded data, some individual characteristics of the observer. These may result in a qualitative loss of data or effect a weighting of certain behavioural items according to the sensitivity, rigour, attitude and position of the primatologist as well as the physical means he has to perceive and record the animals' habits. Tests of inter-observer reliability, which may suggest clues, are not usually practical except in laboratory or confined conditions (Smith & Connelly 1972).

Clearly there are no objective means for describing the mental attitude of the observer and, indeed, few opportunities for other members of the scientific community to judge how important or how variable this is. Psychological and psychophysical properties of the observer may influence the collection of data by recording some activities and not others, or,

by recording some activities disproportionately. Typically observational biases are most important when there are large numbers of animals to be investigated which can not be individually recognised and which are difficult to see (Aldrich-Blake 1970, Chalmers 1968, Clutton-Brock 1972,1974a). It is customary for records to be equalised throughout the active period of the study animals and to choose groups that are not exceptional in the population, although it is almost universal for field biologists to work in areas of high population density - especially if finding the study animals is a major problem (Jolly 1972a).

Behaviour is commonly missed or under-represented in the records if it occurs too quickly, is not obvious, is unexpected or if it happens rarely. Behaviour will be over-represented if it is active, noisy, occurs near to the observer or is otherwise conspicuous.

5.2. Bias and its control in this study.

Bias during the present study arose from a combination of animal 'watchability' and observer movement. Noisy, social activities occurring low in the forest were attended to by the observer who would also preferentially record obvious animals who moved together. Cryptic colouration made even exposed animals difficult to find at first and therefore activities occurring shortly after they had moved were preferentially recorded. This was because (i) animals were 'noticed' as they moved and (ii) they could be identified better as they moved. Movement of individuals away from the observer did not compensate this bias, as the normal locomotor system of habituated Indri involves only short progressions and allows human pursuit.

Having observed one group (Group P) for a month, four specific sources of bias appeared to be affecting the recorded data:

(i) Unequal records were collected for each individual. Alone this is not necessarily the precursor of a bias, but there remained the possibility that specific activities were disproportionately represented in records of rarely seen individuals. Likewise, equal numbers of records do not prove representative sampling but are suggestive of it. If great enough, numerical limitations in the data will alone cause an automatic unpredictable sampling bias through chance effects.

(ii) The possibility existed that specific animals were following the observer. In most rain forest lemurs, the adult male(s) take up positions closer to the potential predator (observer) than other group members. This might bias the observer towards both specific individuals and specific activities.

(iii) Difficulties in remaining with the group consciously manifested itself in a tendency to remain close to the greatest aggregation of animals, predicting the direction of travel or remaining in a central position in the group's geometry. More solitary or peripheral individuals would be discriminated against in subsequent records, or their behaviour recorded mostly when they were close to group members.

(iv) It was recognised early in the study that the observer's relationship with the animals might change during the course of the research. This might be demonstrated in the form of a changing ability to locate or identify individuals or a 'disruptive' effect of the observer when following the group continuously.

It was decided for these reasons, which might vary considerably over the period of investigations, that a standard discipline of observer movement relative to the animals would be enforced, not so as to eliminate bias but to reduce its effects and variability between months.

No animal could be followed continuously throughout a day or a specific period of time and the requirements of the information necessitated latitudinal sampling. Neither could the observer, for reasons outlined above, move randomly about the group. It was essential, therefore, to instigate controls on observer movement that would not only remain invariable between months but would:

a) permit continuous contact with the group under study

b) encourage equal recordings of each individual to be made, or ascribe significance to the relative paucity of records of some individuals' behaviour

c) ensure representative data collection from differently behaving individuals

d) provide an unambiguous observer position for every condition of the group's spatial arrangement.

5.2.1. Group P.

With these four aims in view, a set of general and specific rules were considered, criticised and adapted in practice, and adopted. These remained, for Group P, to dictate data collection for all but the first period of observations (Circuit I). In general the observer was to remain "'inside' the group's dispersion, near the perimeter, towards the future passage direction of the group, near the highest available member of the hierarchy (see below), in a position where most behaviour may be observed." If the group (5 animals) is considered to be distributed about two dimensions only, they in practice always occupied an area as they rarely occurred in a straight line. A commonly occurring situation was 4 animals feeding in 2 or 3 trees with one resting a little further away. As no one animal could be continuously followed the animals were placed into an 'hierarchy'[1] which changed two places

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[1] This 'hierarchy' was constructed by the observer and implies no feature of the animals' behaviour.

each day.

day:	1	2	3	4	5	6	7	8	9	10	(10 days' observations)
most followed	1	3	5	2	4	1	3	5	2	4	
	2	4	1	3	5	2	4	1	3	5	
	3	5	2	4	1	3	5	2	4	1	
least followed	4	1	3	5	2	4	1	3	5	2	
	5	2	4	1	3	5	2	4	1	3	

Each animal, occupying each position in the hierarchy twice during each period of observations, was numbered randomly at the beginning of the first day of each Circuit.

Under optimal conditions the general rule defined above was easily obeyed with a little practice to immediately locate the best position for observation. The observer was not permitted to 'search' continuously for this position. Where group cohesion was not maximal, however, specific rules came into play. These rules, fully described in Appendix 1, had at first to be carried around with the observer. With a few days practice, however, the 'difficult' situations and the required observer movement had been satisfactorily memorized.

All animals were soon equally identifiable and rules had only to be applied for a percentage of the time as there were often no alternatives. The efficiency of the system is examined in Section 8.

5.2.2. Group V.

In order to remain with Group V which contained two adults and an infant, the leading individual had to be closely followed. In practice this was generally the adult female and as interest in this group focused on infant development, the observer normally stayed near to the female and this constituted a potentially important bias. An additional observer was therefore used at one point to calibrate this bias by collecting simultaneous data on the adult male whilst the other observer normally recorded the group's behaviour. The results of this measurement are presented in Section 7.2.1.

During the last Circuit, an hierarchy system, identical to that used throughout for Group P, was employed because the 'infant' had become an independently moving and feeding individual.

5.3. Bias in stationary aspects of recorded behaviour.

Distances between individuals could not be determined on over 80% of all possible occasions, due to wide group distribution and poor visibility. A high proportion of recorded inter-individual distances occurred in relatively rare situations of a cohesive group arrangement e.g. defaecation, earth feeding and feeding on dense food sources. The proportion of records that individuals were seen together, irrespective of distance, is therefore given equal weight to absolute measures of the distance separating them in the following analyses (see Chapter 8).

An animal's position and height could normally be determined even if its activity could not. Initial location of animals high in the tree tops may not have been more difficult than those lower down, as obvious feeding behaviour was generally in progress there. In any case these biases are comparable between individuals and groups although cross-species comparisons should be executed only with caution.

6. THE RECORDED INFORMATION

The development of the various recording techniques used by ethologists has been widely discussed in a recent review by Altmann (1974). The statistical consequences of the system adopted is discussed in a following section, but the methods available to the researcher may be strictly limited by aspects of the behaviour of the animals under study (Clutton-Brock 1972). In the present study such restrictions were in force:

i) Latitudinal sampling was required by the aims of the study.

ii) Continuous rather than point-sample records had to be made of infrequent activities of short duration for sufficient sample size requirements.

iii) The bout length of various behaviours and requirements of observer movement essentially defined the minimum inter-record interval.

A combination of continuous records and point-samples at 5-minute intervals formed the basis of the behaviour recording technique.

6.1. Continuous Records.

All social activities were continuously recorded because they occurred infrequently. Social activities involving contact infrequently occurred during major group progressions and hence recordings were rarely terminated in order to follow specific individuals. Allogrooming, play-wrestling and agonistic interactions were easily seen and heard and were certainly recorded at a frequency superior to that of the percentage time the participants were in view. Absolute measures of the frequency or time spent in social activities are, therefore, difficult to ascertain. Sexual, territorial and scent-marking behaviours were likewise recorded each time they were observed, as were entries to a new part of the home range (see below), the species of food consumed, the presence of other species and any unusual item of information pertaining to the animals' behaviour.

A Hansen-frequency system of recording the number of time periods in which a behaviour occurred at least once was employed, in 5 minute bouts, for activities that were heavily clumped in their temporal distribution but otherwise occurred rarely. If an animal had moved to a different tree since the previous point sample this event was recorded under a category of behaviour 'Previous Activity'. Most primate field studies have included 'travelling', 'moving' or 'locomotion' as behaviour categories designed to measure movement from place to place. The definitive criteria for such behaviour in Indri, with a saltatory and discontinuous form of leaping locomotion, proved difficult to resolve. Small or large movements in feeding trees to achieve a better feeding position were difficult to differentiate from movements culminating in major group progressions, at an early stage in the displacement. With the aid of an additional observer, therefore, attempts were made to collect continuous data on shifts in feeding position in major food trees, the number of leaps and leaping sequences, and the distance travelled in each leap, so as to compensate for the failings of the recording system.

The location of a group in its home range was continuously recorded by its presence in one of about 70 painted quadrats which divided up their ranging areas at ground level. Each quadrat was formed of 50-metre sided squares painted at breast height on selected trees in a ringed pattern of oil-based paints of various colours. The grids were constructed in a north-south and east-west direction, first by one complete set of parallel lines and then by their perpendicular partners. Prismatic compass bearings taken on distant trees, subsequently joined by ropes of unit length, always resulted in the painting of squares whose sides varied by no more than 5 metres in 50 metres. Grid size discrepancy was not therefore sufficiently great to warrant separate measurement (Clutton-Brock 1972). No paths were cut in the forest if these could be avoided, as previous observations had indicated that Indri used saplings as an important source of food.

It was considered sufficient for major differences in ranging behaviour to be adequately recorded by quadrat entries (see below), home range utilisation by quadrat occupation measures, and the diversity of local movements by tree changing frequency and the numbers of leaps performed.

In addition, the event of the observer having to make a major adjustment in his position was recorded a maximum of once for each 5 minute period.

The ridged structure of parts of both study groups' ranging areas caused the type and structure of plant species to vary considerably. Grid systems should not, therefore, be considered as dividing an area into equal portions. Similarly, the undulations of canopy in the montane forest buffered the underlying topographical structure due to ridge-top trees being small and valley-living trees tall. Ground measured quadrats on slopes may possess a different ecological significance from those in flat regions.

6.2. Point-Sampled Data.

Each individual's activity, whether the individual was identified or not, was recorded at 5-minute intervals. Each identified record constituted an 'IAR' (Individual Activity Record). This system of recording was designed primarily to estimate the proportion of time spent in feeding and in the subsequent analysis non-feeding activities are generally considered together. Foraging for food was recognised in *Indri* from time to time and may have been a major activity, but no satisfactory definition could be determined to certify its presence. Richard (1973) concluded similarly in her study on *Propithecus verreauxi*.

Information concerning the spatial arrangement of the group, the positions and the heights of animals in the trees were collected during the study. Every 5 minutes on the point sample, the height of each animal was estimated by eye. The inaccuracy of height estimations has been mentioned by Clutton-Brock (1973), who retrospectively measured a consistent <u>underestimation</u> and subsequently utilised a correction factor in data analysis. In Madagascar height measurement was practised continually throughout the study but quantitative observations were not begun until calibration with a Zeiss altimeter proved that the considerable initial underestimations (found to be proportional to height) were within a 10% error.

In order to investigate which parts of the trees were most used by <u>Indri</u>, measures of the animals' positions in or underneath the canopy were taken. Clutton-Brock (1972), in an exemplary attempt to calculate foliage or food-containing 'cover' in the forest at Gombe Stream Reserve in Tanzania, made the generalisation that woody vegetation was covered by cylinder-shaped canopy structures. This was not true for the evergreen vegetation of the Malagasy rain forest. It was, possible, however, to recognise three geometrical forms, slight variations on which accounted for most of the food trees' shapes:

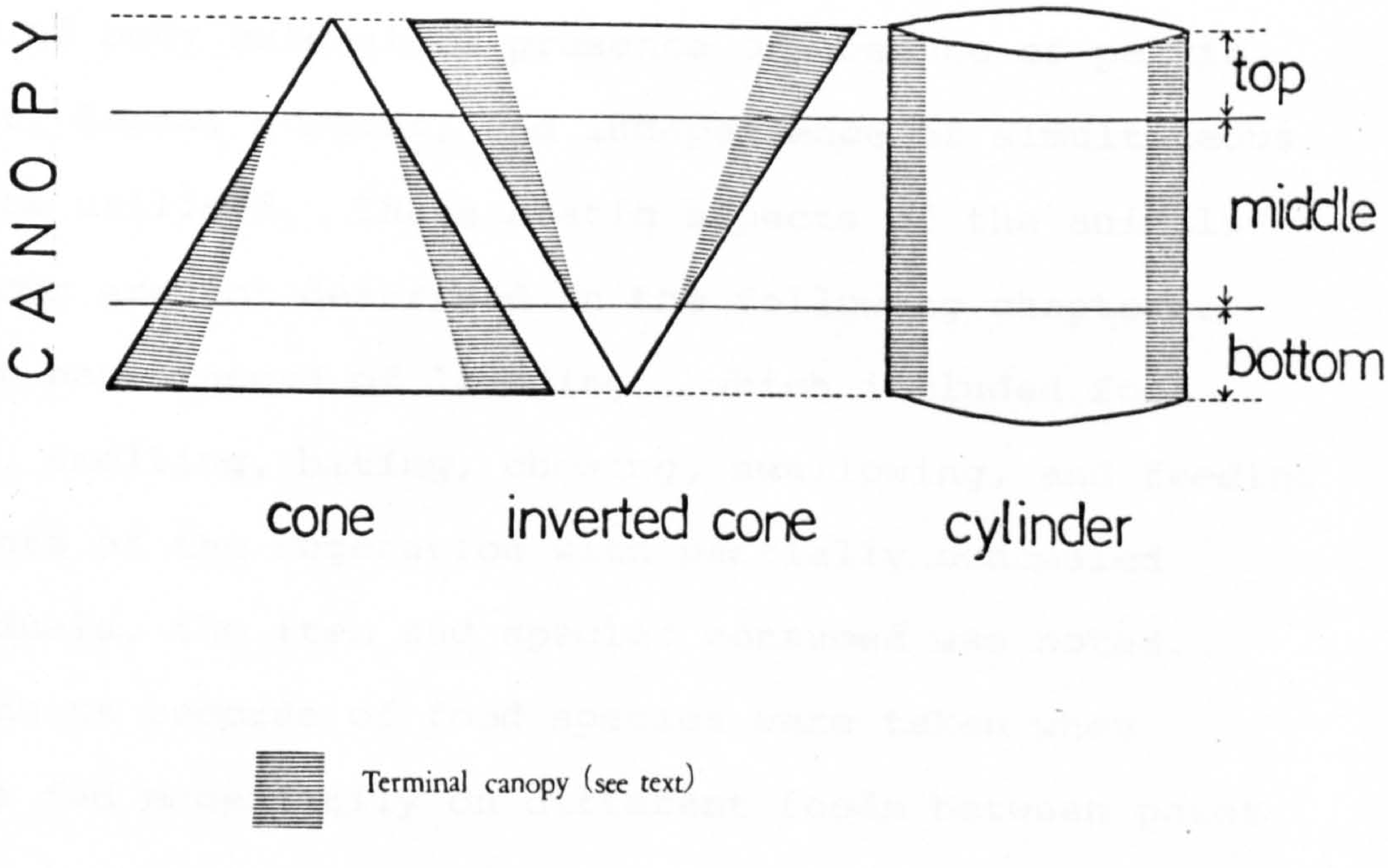
(i) cone (ii) inverted cone (iii) cylinder

Cylinder-shaped foliage structures were rarely encountered and were generally confined to a single family (Guttiferaceae). The canopy of trees of all heights was divided into vertical divisions independent of tree height, the central portion ('middle canopy') representing approximately half the canopy height, and the top ('canopy top') and bottom ('canopy bottom') each one quarter. Horizontal divisions were made according to the potential of the animals' feeding position. Thus if the animal was placed so that it was able to feed, without moving, on the most lateral parts of the foliage, this was scored as a 'terminal' position. The canopy of each tree was therefore divided up into between 3 and 6 positions (Fig. 2.3). These positions were unambiguous i.e. if the animal was situated in the centre of a small tree and yet able to feed on the extremities from that position, then it was <u>not</u> considered to occupy a terminal position. A final category 'underneath canopy' concluded the range of possible animal positions.

No criteria could be found to define the position of food in the trees. The periphery and 'terminal' regions appeared to be relatively well endowed with food items but these were also the easiest to see. In some species fruit size varied according to canopy position and some trees simultaneously possessed fruit from two different fruiting seasons possibly years apart (e.g. <u>Symphonia clusoides</u>). Young leaves were likewise distributed and it was decided that attempts to quantify the forest's food production would be prohibitively inaccurate.

Every 15 minutes all visible inter-individual distances were estimated and recorded in the form of a group plan on the check sheet. Inter-individual distances

Figure 2.3 Divisions of the three main tree canopy types into 'canopy top', 'canopy middle' and 'canopy bottom', and 'terminal canopy' positions.


CANOPY
top
middle
bottom
cone
inverted cone
cylinder
▨ Terminal canopy (see text)

were not recorded in predetermined categories so as to permit subsequent cross-species comparisons.

Parameters of rain, wind and cloud cover were also recorded at 15-minute intervals. Rain and wind were each assigned to one of 5 categories and cloud cover estimated in the form of a percentage cover of sky immediately overhead. In the following analyses only dry, light or heavy rain conditions are considered.

Data were also collected concerning the posture of the animals, the diameter and angle of the supports used, degree of body extension, presence or absence of pelvic support, dorsal support, and independence of simultaneous supports utilised. These static aspects of the animals' behaviour are not described in the following chapters.

At each record of 'feeding', which included food nosing, smelling, biting, chewing, swallowing, and feeding movements of the vegetation with partially concealed individuals, the item and species consumed was noted. (Continuous records of food species were taken when animals fed momentarily on different foods between point samples.) Feeding was a continuous activity as the animals reached for and picked food whilst still chewing and swallowing the last item. The approximate age and colour of the food items were also recorded. 'Resting' included all other non-active behaviours and any other activities were unequivocal in definition and recognition.

6.3. Population data.

Indri groups communicate with each other by means of frequent loud calls. The vocalisations of all Indri groups were continuously recorded on the check sheets. A compass bearing of the calls' origins, estimation of distance (see Chapter 9), location of the observer, call duration, number of individuals vocalising, call type and reply type (see Chapter 9), weather conditions and duration of groups of calls, were recorded at all times in all three study areas.

Qualitative aspects of the behaviour of other Indri groups and sympatric lemurs were recorded at Maromizaha, Fierenana and other visited forests.

On occasions, standard sampling techniques had to be dropped. Fast and long group progressions or inter-group encounters either necessitated ceasing data collection altogether or (rarely) the adoption of continuous recording techniques. These interruptions in data collection accounted for the loss of no more than 5% of the maximum recordable behaviour (see Section 8).

7. STATISTICAL TREATMENT OF NUMERICAL INFORMATION

7.1. Introduction.

Statistical treatments of ethological data are commonly encountered in reports of animal sighting, group composition, individual or age/sex class behaviour and temporal, seasonal or reproductive variability in the frequency of behavioural events. An assumption that few ethologists question is that of independence of samples in compared populations, a pre-requisite to both parametric and non-parametric analytical techniques. Criticism has been levelled against the use of X^2 tests by Buxton (Struhsaker 1969) and Crook & Aldrich-Blake (Clutton-Brock 1972). In both these examples, the proportions of sighted members of the primate group engaged in various activities were compared at different times of the day. Sampling techniques involved whole group scans at 5-minute intervals and probably involved successive records of the same individuals whose behaviour might not have meanwhile changed. This, according to Siegel (1956), results in an 'inflated N' although no formal definition of the problem or its solution is offered.

What exactly, one may ask, constitutes statistical independence? Feller (1950,page 86) defines it as follows: ....." two events A and H are said to be statistically independent if Pr[1]/AH/ = Pr/A/. Pr/H/ .... statistical

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[1] Probability

independence implies that no inference can be drawn from the occurrence of H to that of A ...". There are some objections to simple definitions of mathematical independence in practice. Clutton-Brock (1972) takes an inter-point sample interval of 15' as satisfactory, as there was reason to believe that successive scans of a group of Colobus badius involved observations of different animals. No measurement was made, however, of the frequency of observation of any one individual.

One approach has been to use inter-sample intervals greater than the bout length of the longest occurring behaviour. Oates (1975) and Struhsaker (1974), for example, made successive behavioural records on the same individuals only if (a) their behaviour had meanwhile changed, or (b) a sufficient time interval (60 minutes) separated successive observations. A consequence of (a) above is that short bouts of behaviour following long ones would be proportionately over-represented although this source of bias was reduced by requiring recorded behaviour to last at least 5 seconds, thus bringing another potential bias into play. An additional criticism of this recording method is that animals frequently changing their behaviour would be most represented in the data.

Chalmers (1968) used 30 minutes as the inter-record interval but neither he nor Clutton-Brock attempted to measure the relationship between bout length of the behaviour under study and the interval betwen successive records.

Changes in the behaviour of an individual, or a selected change of individual by the observer, between successive records, may not in themselves confer independence on the data, as the members of socially living primate groups organise their behaviour in an essentially dependent fashion, both temporally and amongst each other.

In this study various point sample intervals were examined and successive records tabulated in the form of point sample transition frequencies. These could be tested against transitions expected from chance associations. Results and criticism of this approach are presented in the following section.

7.2. Problems associated with the representativeness and independence of behaviour recorded in the study.

7.2.1. Representativeness.

Due to the behaviour of the animals and the limited visibility through the environment records tended to be made in groups. According to the laws governing the changes of position made by the observer, notably that prohibiting searching movements to achieve an optimal position, animals seen at time 't' were those most likely to be seen at time 't+1'. The possibility that data 'clustering' influenced estimates of the proportion of time spent in two major activities "feeding" and "not feeding", was examined by the use of a second observer. The additional observer was instructed to remain as long as possible with one specific individual, whilst the first observer recorded the group's behaviour according to the system described in Section 5.2.1. In this way non-clustered or 'complete' data could be compared with clustered or 'sporadic' data. An additional function of the simultaneous recording technique was that the behaviour of the Group V adult male, who was normally seen only when close to the female, could be monitored whilst out of sight of the first observer and therefore far from the adult female. This would permit a greater certainty to be placed on behavioural differences located in inter-individual comparisons by the first observer throughout the year.

At precisely the same 5-minute points, both observers recorded the activity of the subject. The habituated state of the animals at this time (March 1973) was such that the presence of another observer interfered little with their behaviour. Differences in the observed proportion of time spent feeding recorded by the two observers could then only be attributed to two factors:

(i) Real differences in the subject's behaviour when in or out of sight of the main observer,

(ii) Inherent variability, due to techniques of data recording, deriving from specific biases (see Section 7), the chance influence of sampling procedures, and the effects of clustered data.

<u>Results</u>: (i) <u>Group V</u>: The observer (No.1) remaining continuously with the adult male for the seven days'

observations kept him in sight for 84.9% of the time that the group was active, compared to 46.3% for Observer No.2. Their respective measures of the mean percentage time spent feeding were 27.6% and 22.3% and these differences were not significantly different ($X^2(1d_f) = 0.4261$. $0.5<p<0.7$).

(ii) Group P: Continuous recordings on Group P individuals were insufficient in number to analyse individually. Observer No.1 (continuous) remained in view of the subject for a mean of 83.2% of the active period, and Observer No.2 (sporadic) for 26.4%. The respective mean proportions of time spent feeding were for O1, 42.5% and for O2, 49.0% ($X^2_{(1df)} = 1.1004$. $0.2<p<0.3$).

As inter-observer reliability appeared to be high despite the different proportions of time the two observers saw the subject, the effect of data clustering (and other biases) and distance-dependent variability in the Group V adult male's behaviour appeared to be minimal. It is considered likely, therefore, that estimates made by a single observer of the proportion of time spent in feeding and 'other' activities by each individual were probably representative.

7.2.2. Independence.

As no satisfactory precedent for defining statistical independence was encountered in the psychological and statistical literature, the following procedure was devised: For both 'complete' and 'sporadic' data, point sample transition matrices were drawn up for successive records separated by 5, 10 and 15-minute intervals. The minimal inter-point-sample interval that conferred no statistically verifiable dependence was searched for and tested against chance expectations by a X^2 contingency table using one degree of freedom. According to Miller & Frick (1949, page 313) this approach is justified ...." according to the assumption of independence if the relative frequencies of response A is p(A)=0.5, and of response B is p(B)=0.5, we could assume that the relative frequencies of A (followed by)*A, of B (followed by) B, of A (followed by) B and of B (followed by) A are all 0.25, and of triads are 0.125 etc. If an actual tabulation of sequences shows significant departures from these values then the assumption of independence is not justified, and the frequency distributions for sequences of 'n' responses cannot be derived from the distribution for individual responses ... "

Results: Only activities of feeding (F) and 'not feeding' (NF) are considered and the data used is of the Group V adult male who was apparently not exceptional in this respect.

In Table 2.10, for both clustered and complete data, only 15-minute sampled information represent records which are not significantly dependent. It is recognised that showing successive records not to be significantly dependent may not justify their nomination as truly independent records, but no criteria are available to make this

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* my parentheses

decision. In all cases where statistical treatments are employed in the following chapters only records separated by at least 15 minutes are involved.

It could be reasonably argued that major properties of primate societies lie either in the synchrony of behaviour between individuals or in the widespread significance of communicative actions represented as facilitation or inhibition of one (or more) animal(s) by another (or others). Theoretically no scan should therefore contain more than a single individual's behavioural record, since social communication 'inflates sample size' when whole groups are to be compared. There is no solution to this problem without:

(a) invoking an immeasurable bias on the data - for example, how is the single record to be chosen?

(b) reducing the data to non-comparable proportions.

Reasonably stringent levels of significance ($p<0.05$) are therefore employed and similar degrees of intra-group behavioural dependence proposed in mitigation.[1]

In the course of defining the arguments presented above, an alternative approach presented itself, and with the aid of a statistician (J. Robinson, pers. comm.), a method using the dependence itself to calculate overall proportions of time spent in various activities (and ascribe standard errors to their distributions) evolved (Appendix 2). The system proposed was not directly

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[1] The use of the X^2 test is widespread in the following chapters. Differences are only tried within groups when it has been already shown that the constituent values are significantly heterogeneous. Thus the adult male would not be tested against the adult female unless there was a significant variation in the measure throughout the group.

Non-parametric tests do not assume an underlying distribution and, therefore, no test for heterogeneity is required.

(although it is potentially) appropriate for machine computation and is not used in the following discussions of Indri behaviour.

8. QUANTITATIVE OBSERVATIONS ON INDRI INDRI

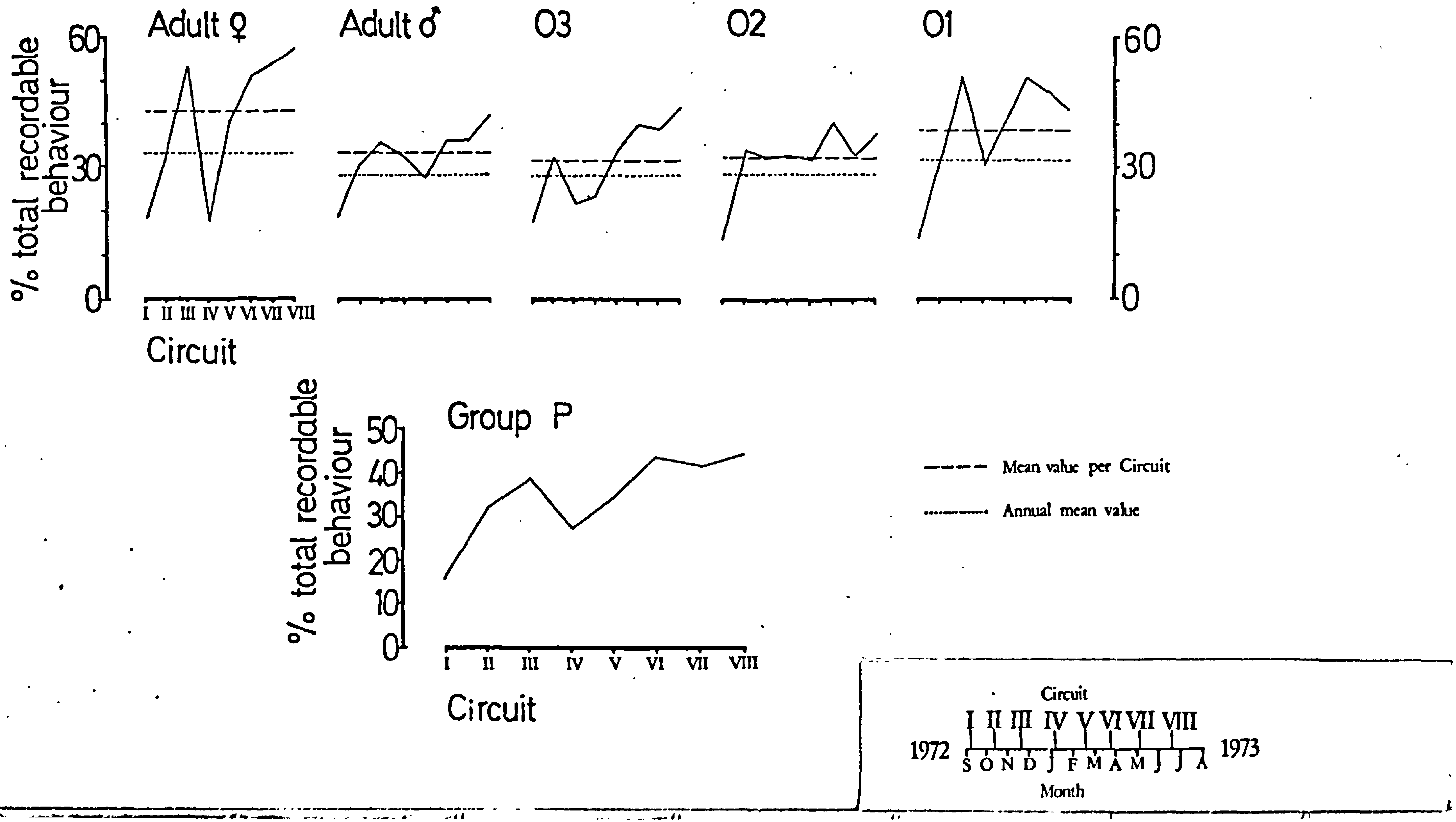
8.1. Group P

Despite attempts to equalise the observations for each individual (see Section 5.2.1), each member of Group P was seen differently during the active period of the group. Consistent inter-individual differences in 'watchability' are not the topic of this chapter, but Figure 2.4a shows the approximate similarity of IARs recorded for each animal during each period of observation. The low initial amounts of behaviour recorded (Circuit 1) were due not to difficulties in finding animals but to a restricted ability to identify individuals (see Table 2.2). The adult female of this group, wounded in the back between Circuits III and IV was unable to follow the group for some days and remained solitary and immobile throughout much of the (Circuit IV) activity period. This not only affected the numbers of records of her behaviour, but also those of her youngest offspring (O1) who normally stayed close to her.

The increasing overall trend in identified IARs throughout the period of research was at least partly due to improvements in identifiability of the animals (Table 2.3). A change in group cohesion would be manifested in differences between Circuits in the numbers of animals

<u>Figure 2.4a</u> Seasonal variation in the proportion of recordable behaviour obtained for each individual in Group P, and for the whole group. The value for each individual each Circuit is expressed as a % of the maximal recordable behaviour had each individual been seen on every point-sample during the Circuit.

(see page 58 for Figure 2.4b)


Adult ♀
Adult ♂
O3
O2
O1
% total recordable behaviour
60
30
0
I II III IV V VI VII VIII
Circuit
Group P
% total recordable behaviour
50
40
30
20
10
0
I II III IV V VI VII VIII
Circuit
Mean value per Circuit
Annual mean value
Circuit
I II III IV V VI VII VIII
1972
S O N D J F M A M J J A
1973
Month

CIRCUIT	I	II	III	IV	V	VI	VII	VIII
N	1424	1957	2647	1970	2119	2590	2344	2482
n	810	201	322	332	236	236	184	55
%	56.9	10.3	12.0	16.9	11.1	8.9	3.4	2.1

TABLE 2.2. Annual distribution of unidentified records (n) as a percentage of all records (N) for Group P.

CIRCUIT	I	II	III	IV	V	VI	VII	VIII	TOTAL
n	481	1488	1912	1492	1609	1741	1699	1652	12074
N	2690	4670	4880	5260	4325	3970	3935	3430	33160
%n	17.9	31.7	39.1	28.2	37.3	43.8	43.1	48.3	36.4
%N	47.9	39.7	43.2	34.4	44.8	49.7	45.4	49.9	43.6

TABLE 2.3. Summary table of the annual distribution of identified (%n) and total (%N) recorded behaviour as percentages of total amount of recordable behaviour(N) in Group P (5-minute points).

CIRCUIT	I	II	III	IV	V	VI	VII	VIII	TOTAL
n	181	277	336	252	210	208	237	206	1907
N	286	390	484	356	384	370	316	298	2884
%	64.2	71.1	69.6	70.8	54.7	56.2	75.0	69.2	66.4

TABLE 2.4. Summary table of the annual distribution of percentage recorded behaviour in Group V (15-minute points).

seen at each scan (Fig.2.5a/b), but no consistent trend is evident beyond an improvement in the number of scans in which at least one individual was seen.

Seasonal variation in the amount of behaviour (Fig.2.4a) recorded was not revealed clearly through the trends described above (despite considerable differences in the activity period - see Chapter 3), either for the group or individuals. In summary (Table 2.3) sufficient numbers of records for each individual were collected during each Circuit for statistical purposes. Overall, 43.6% of the maximum recordable behaviour[1] of this group was gathered although only 36.4% could be ascribed to specific individuals. 83.5% of all records of behaviour identified individuals.

8.2. Group V.

The proportion of records of behaviour collected from Group V individuals varied from 60.6% to 77.2% for the adult female and from 46.1% to 72.8% for the adult male. The infant is considered separately in Chapter 10 .

Although the observer followed the adult female almost exclusively, the adult male was also often seen (Figure 2.4b) and due to the small group size and cohesive structure 66.3% of the total recordable behaviour was obtained.

All records were identified (the animals were quite differently coloured) and no seasonal variation in the

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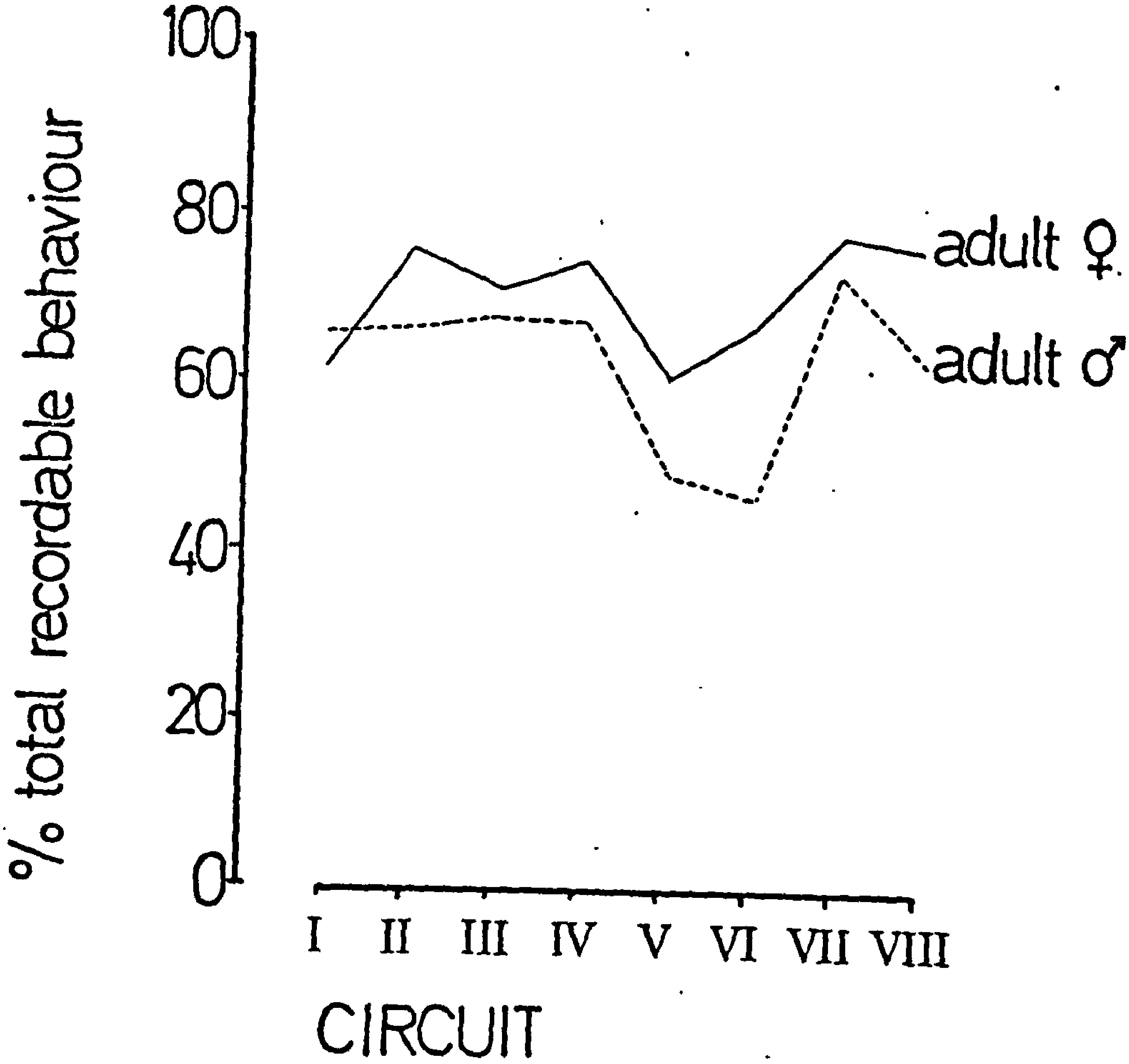
[1] The maximum recordable behaviour is the total number of IARs obtained had the behaviour of all group members been recorded at every point-sample.

Figure 2.4b Seasonal variation in the proportion of recordable behaviour obtained for each individual in Group V. The value for each individual each Circuit is expressed as a % of the maximal recordable behaviour had each individual been seen on every point-sample during the Circuit.


100
80
60
40
20
0
% total recordable behaviour
adult ♀
adult ♂
I
II
III
IV
V
VI
VII
VIII
CIRCUIT

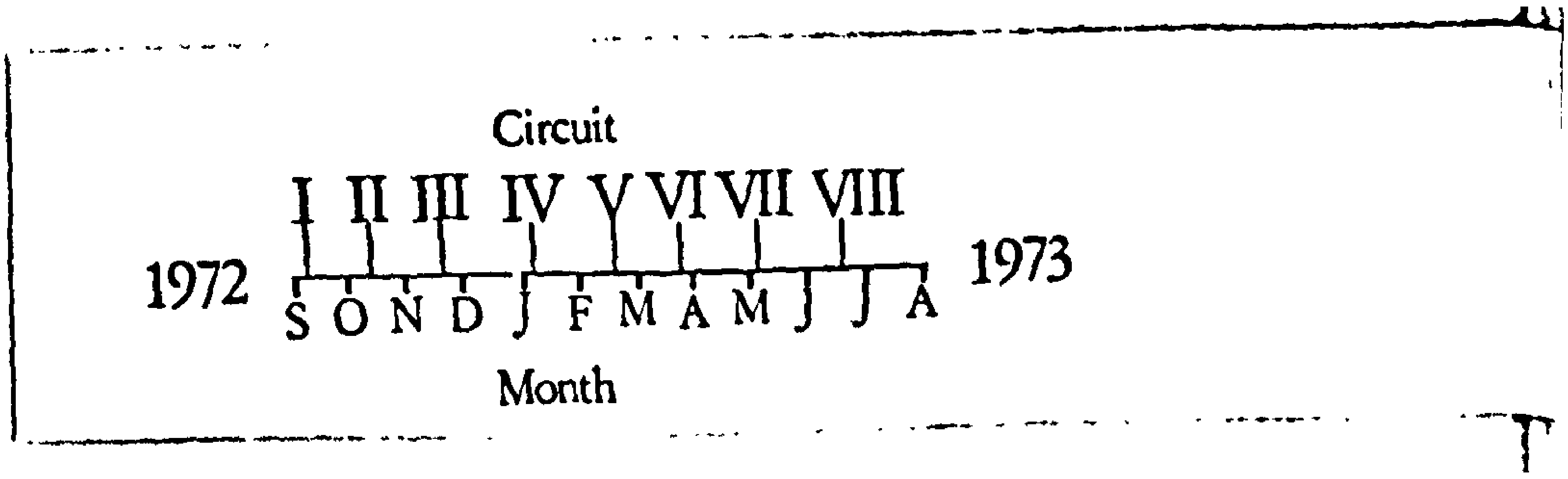
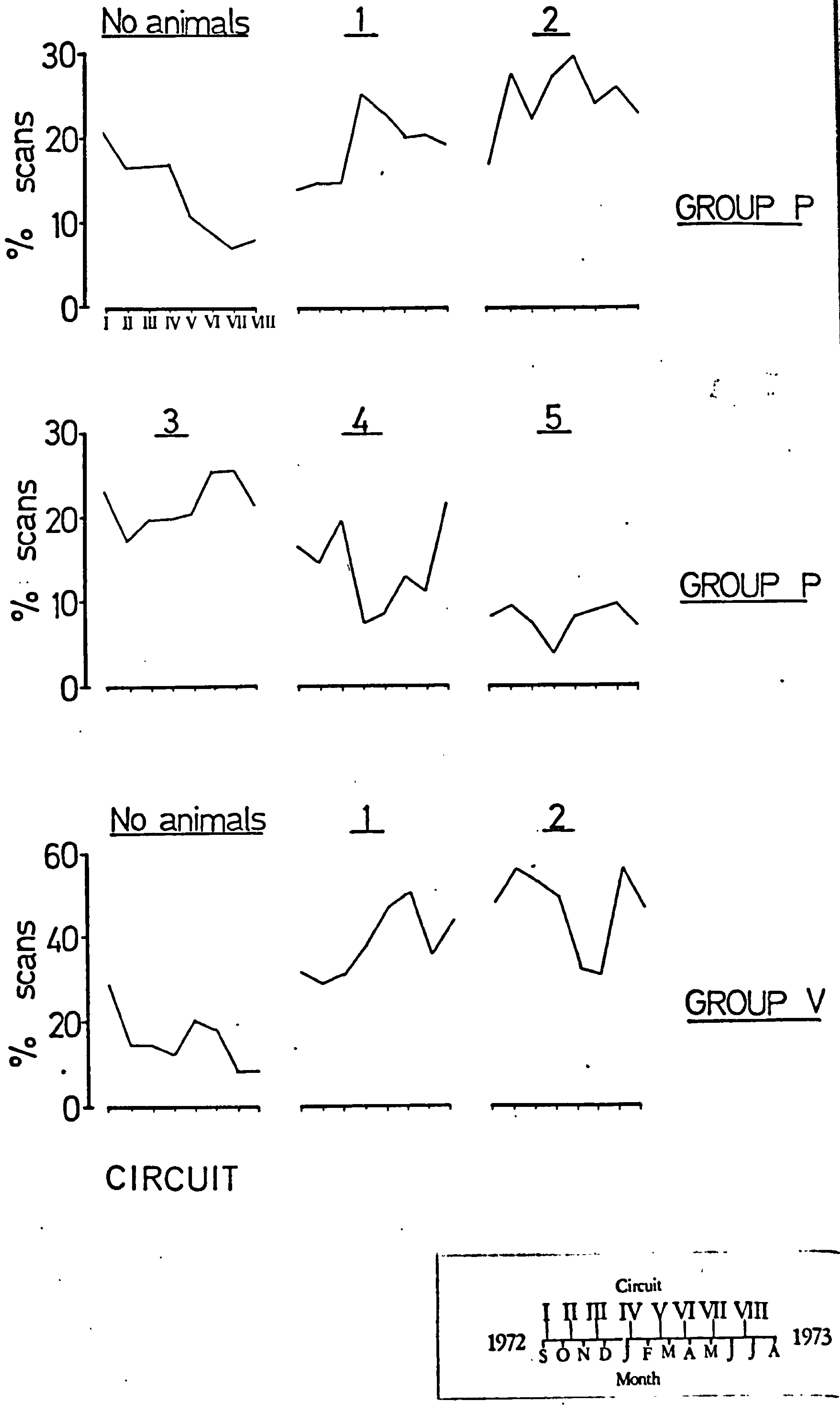
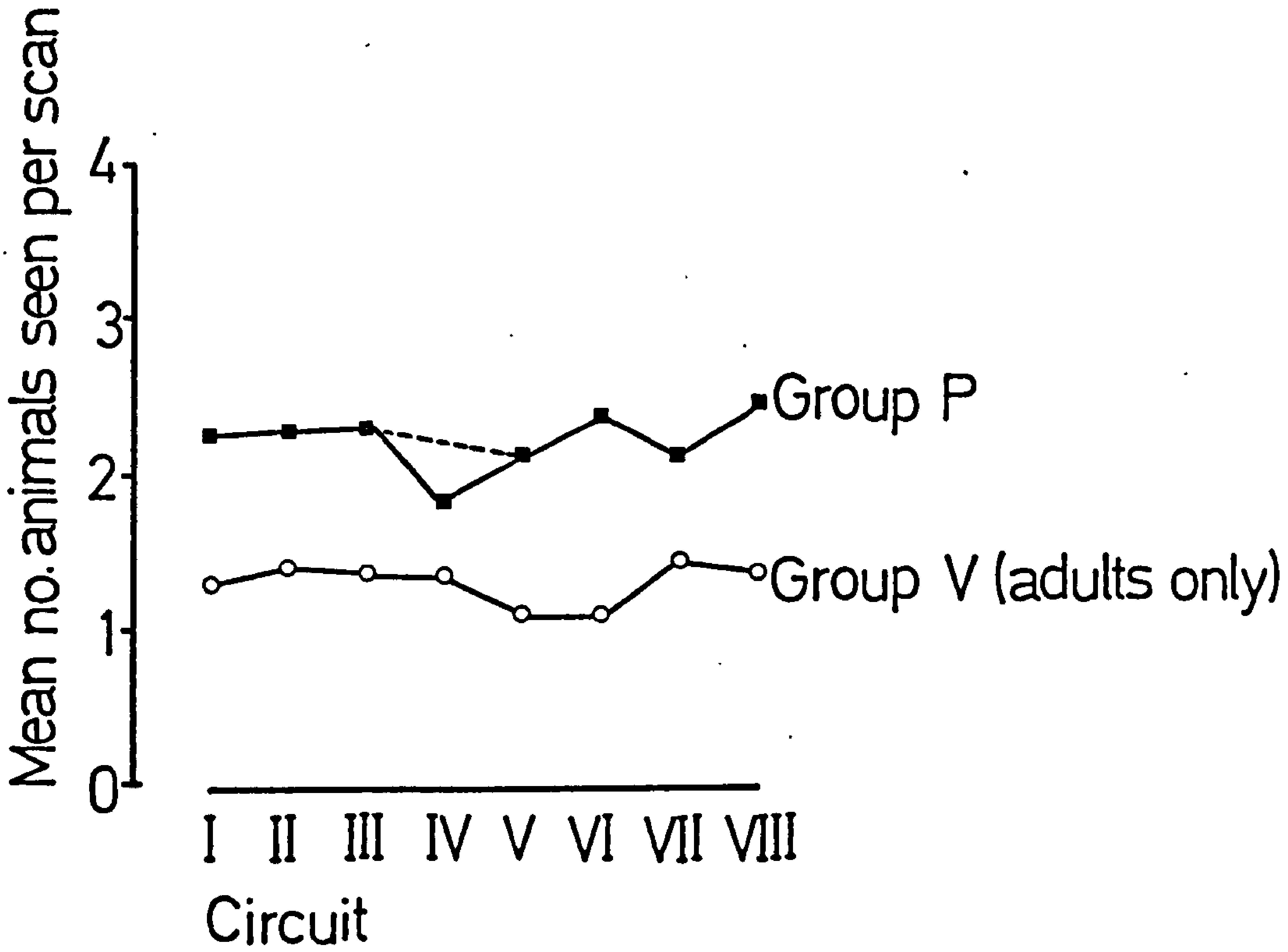
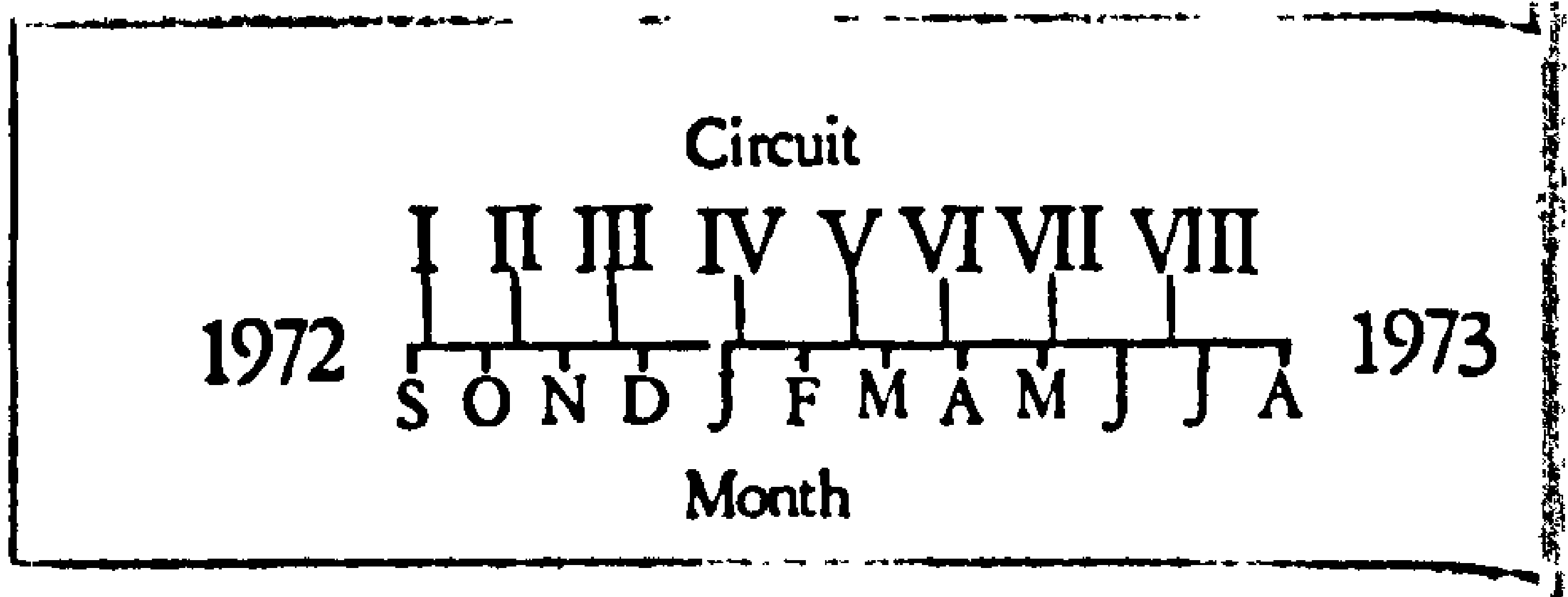

Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
1973
Month

Figure 2.5a Seasonal variation in the numbers of individuals seen in scans of Group P and Group V.


No animals
1
2
GROUP P
3
4
5
GROUP P
No animals
1
2
GROUP V
% scans
30
20
10
0
60
40
I II III IV V VI VII VIII
CIRCUIT
Circuit
I II III IV V VI VII VIII
1972
S O N D J F M A M J J A
1973
Month

<u>Figure 2.5b</u> Seasonal variation in the mean number of animals seen per scan in Group P and Group V.


Mean no. animals seen per scan
4
3
2
1
0
Group P
Group V (adults only)
I
II
III
IV
V
VI
VII
VIII
Circuit


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
1973
Month

amount of information recorded was evident. Both individuals were seen rather less during Circuits V and VI than at other times of the year (Table 2.4 , Fig. 2.5a/b).

8.3. Efficiency of the sampling technique for Group P.

The success of the variable 'hierarchy' sampling technique used for observations on Group P may be measured by examining the relative numbers of records achieved for each individual on days when it was the most followed individual, and comparing these with records collected on other days. The ratio of these two measures is called the Sampling Efficiency Ratio (SER), and its values for each individual per Circuit are shown in Table 2.5 . Figures for Circuit IV when the sampling system was disrupted by the adult female's wound are not presented. During Circuit I 'random' observer movement was in operation and individuals were seen equally between days although some individuals were consistently seen more than others.

The SERs may be seen to vary greatly between individuals, but no consistent seasonal trend is evident. As the same rules applied for each individual, this variation must represent differences in animal behaviour or the observer's perception or identification. There was no reason to believe the sighting or recognition of individuals varied considerably.

As expected, the value of SER negatively correlates perfectly with the overall numbers of IARs recorded for each individual. The animals that were most seen overall,

CIRCUIT	Ad♀	Ad♂	03	02	01
II	0.42	2.48	2.13	1.80	1.95
III	1.31	2.04	2.11	1.26	1.77
V	0.95	1.87	1.56	1.11	2.04
VI	1.67	1.87	2.53	2.24	0.97
VII	1.67	2.16	2.56	1.89	1.46
VIII	1.27	1.78	1.74	1.62	1.29
TOTAL	1.22	2.03	2.04	1.62	1.55

TABLE 2.5. Individual and seasonal variation in sampling efficiency ratio (SER) in Group P.

INDIVIDUAL	ΣX	$\bar{X}$	SD	SE	n
Ad♀	540	90	37.4	15.3	6
Ad♂	602	100.3	18.9	7.7	6
03	655	109.2	17.0	6.9	6
02	537	89.5	14.7	6.0	6
01	602	100.3	19.1	7.8	6

TABLE 2.6. Individual variation in the total numbers of records collected on top hierarchy days in Group P.

therefore, were affected less by the adopted following techniques than those seen less often. From Table 2.6 it can be seen that during the days in which specific animals were most followed there was little variation in the absolute numbers of IARs recorded between individuals. It was, therefore, the relatively poor observation of some individuals during days in which they were low in the hierarchy that individual differences in 'watchability' were established. It was the adult male and oldest male offspring (see Chapter 5) that were exceptional in this respect.

It was probable that spatial rather than activity differences caused this variation as the adult female and the younger animals were more often seen together and formed an easily observable association. The oldest male offspring and adult male were consistently those individuals most often seen alone in a group scan (Table 2.7). It is unlikely that this spatial displacement of each of these two animals from the rest of the group was acute as the numbers of records of <u>other</u> group members collected whilst they were followed, were similar (Table 2.8), and the number of times the observer had to change his position whilst following them was not exceptional (Table 2.9).

8.4. Diurnal variation in data collection.

(a) Group P

The group's daily number of IARs did not vary extensively between Circuits (Figure 2.6). An exception to the peak in the warm, wet summer (Circuit III) when overall

INDIVIDUAL CIRCUIT	Ad♀	Ad♂	03	02	01	TOTAL
II	9.8	23.0	16.4	10.1	9.0	15.9
III	8.2	10.0	14.3	11.6	5.3	9.4
IV	36.7	24.7	14.3	15.8	11.4	20.3
V	8.7	14.5	17.3	7.0	8.1	11.1
VI	9.7	12.8	10.9	9.1	6.2	9.5
VII	8.4	20.2	9.0	9.6	4.4	10.0
VIII	9.1	11.9	11.6	13.3	3.7	9.9
TOTAL	10.8	15.9	13.1	10.7	6.6	11.3

TABLE 2.7. The % of each individual's IARs that they were seen alone each circuit.

INDIVIDUAL	ΣX	$\bar{X}$	SD	SE	n
Ad♀	1914	159.5	39.7	11.5	12
Ad♂	2082	173.5	39.7	11.4	12
03	2222	185.2	48.3	13.9	12
02	2509	179.2	39.2	10.5	14
01	2242	160.1	28.9	7.7	14

TABLE 2.8. The number of records of the behaviour of other group members when each individual was top in the hierarchy.

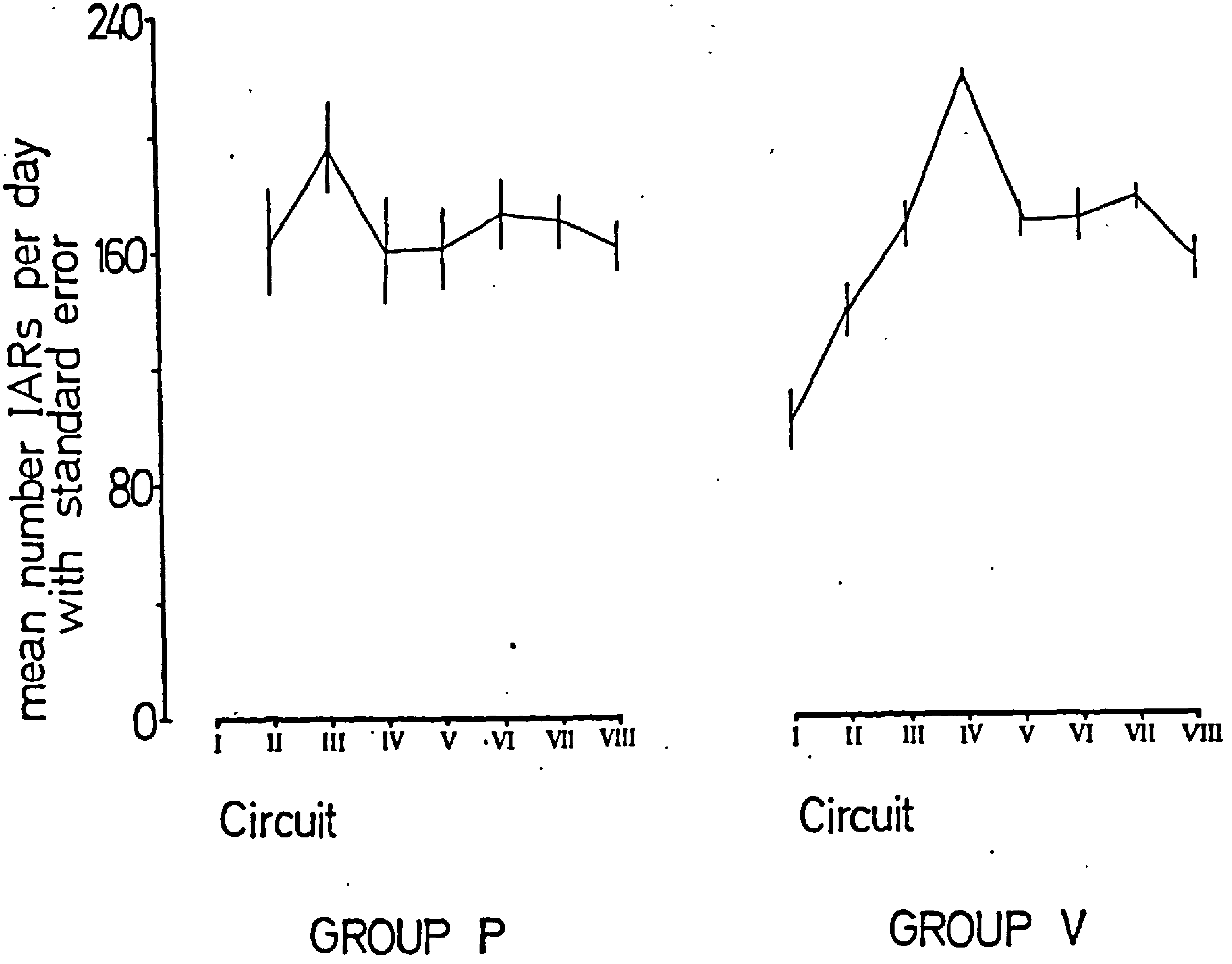
INDIVIDUAL CIRCUIT	Ad♀	Ad♂	03	02	01	TOTALS
II	-	-	47	44	45	-
III	53	58	40	40	49	240
V	55	42	28	58	65	248
VI	48	67	47	34	69	265
VII	56	49	52	66	45	268
VIII	38	43	55	52	59	247
Totals	250	259	269	294	332	
$\bar{x}$ / day	25.0	25.9	22.4	24.5	27.7	

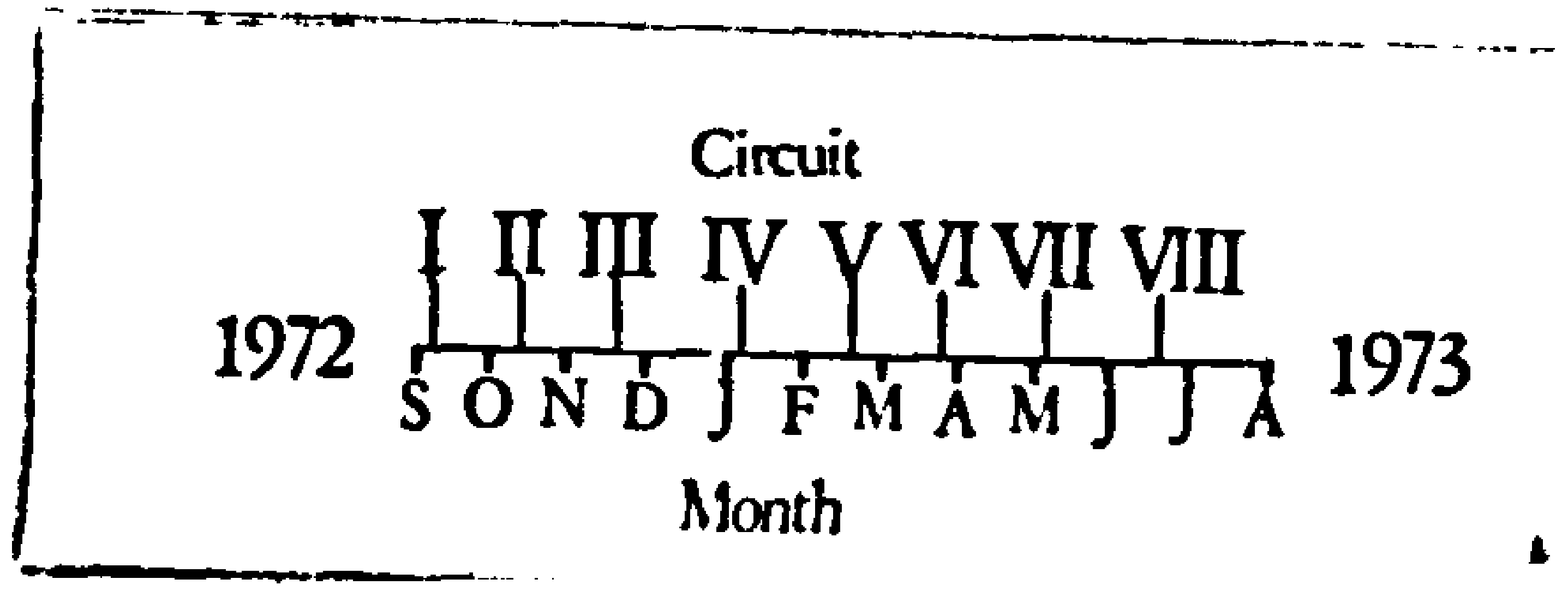
TABLE 2.9. The numbers of 5-minute periods in which the observer had to move in order to record top hierarchy individuals.

	TIME INTERVAL					
	Complete			Sporadic		
TRANSITION	5'	10'	15'	5'	10'	15'
F - F	60	21	12	25	6	5
F - NF	37	27	22	17	7	8
NF - F	34	25	20	11	6	6
NF - NF	231	100	58	98	49	25
TOTAL	362	173	112	151	68	44
$X^2_{(1df)}$	82.8	9.91	1.085	40.88	8.93	1.782
p	<0.001	<0.01 >0.001	<0.3 >0.2	<0.001	<0.01 >0.001	<0.2 >0.1

TABLE 2.10. The independence of records made at various time intervals for both complete and sporadic data. Data from one individual (the adult male of Group V). Complete data contained 89.7% and sporadic data contained 51.9% of all possible records.

Figure 2.6 Daily variation in the mean numbers of Individual Activity Records (IARs) obtained in each group for each Circuit.


240
160
80
0
mean number IARs per day with standard error
I
II
III
IV
V
VI
VII
VIII
Circuit
GROUP P
I
II
III
IV
V
VI
VII
VIII
Circuit
GROUP V


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S O N D J F M A M J J A
1973
Month

activity related to the increased daylength, occurred in Circuit IV due to the segregation of the adult female from movements of the rest of the group (see Chapter 8).

(b) Group V

No seasonal trend in the daily number of IARs in Group V (Fig.2.6) can be supposed because for this group other factors influenced active day length (see Chapter 3).

8.5. The temporal distribution of recorded data.

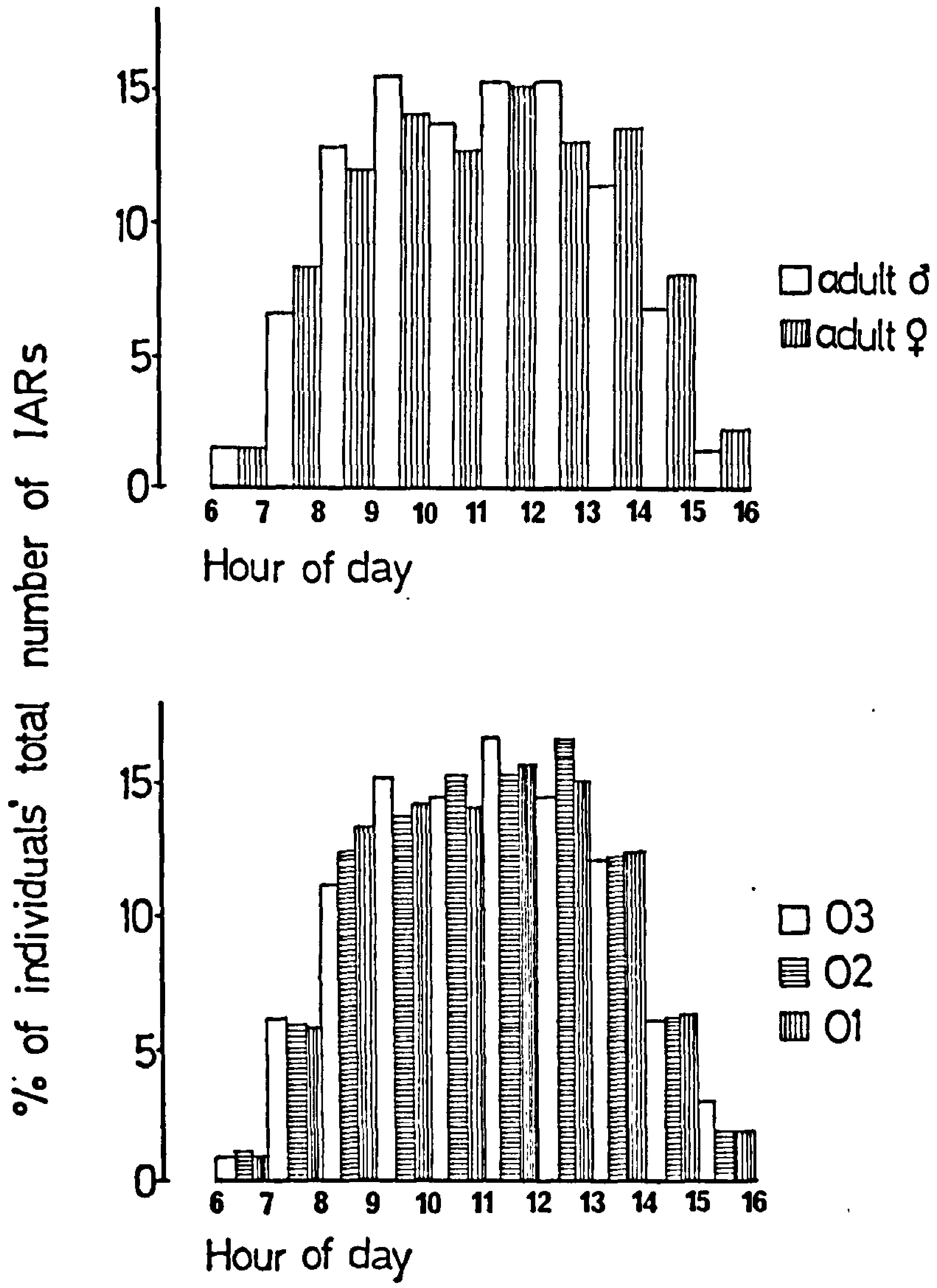
Only all-day follows were employed in this study and the distribution of IARs therefore reflects aspects of animal behaviour. Altmann & Altmann (1970) accounted for some 'artefacts' in their data by the tendency for the observers to rest at midday. Clutton-Brock (1972) also sometimes rested at midday, but recorded enough behaviour to make statements about the activities of the animals at these times.

In this study in both groups the observer remained with animals from at least 30 minutes before activity began to at least 30 minutes after activity ceased.

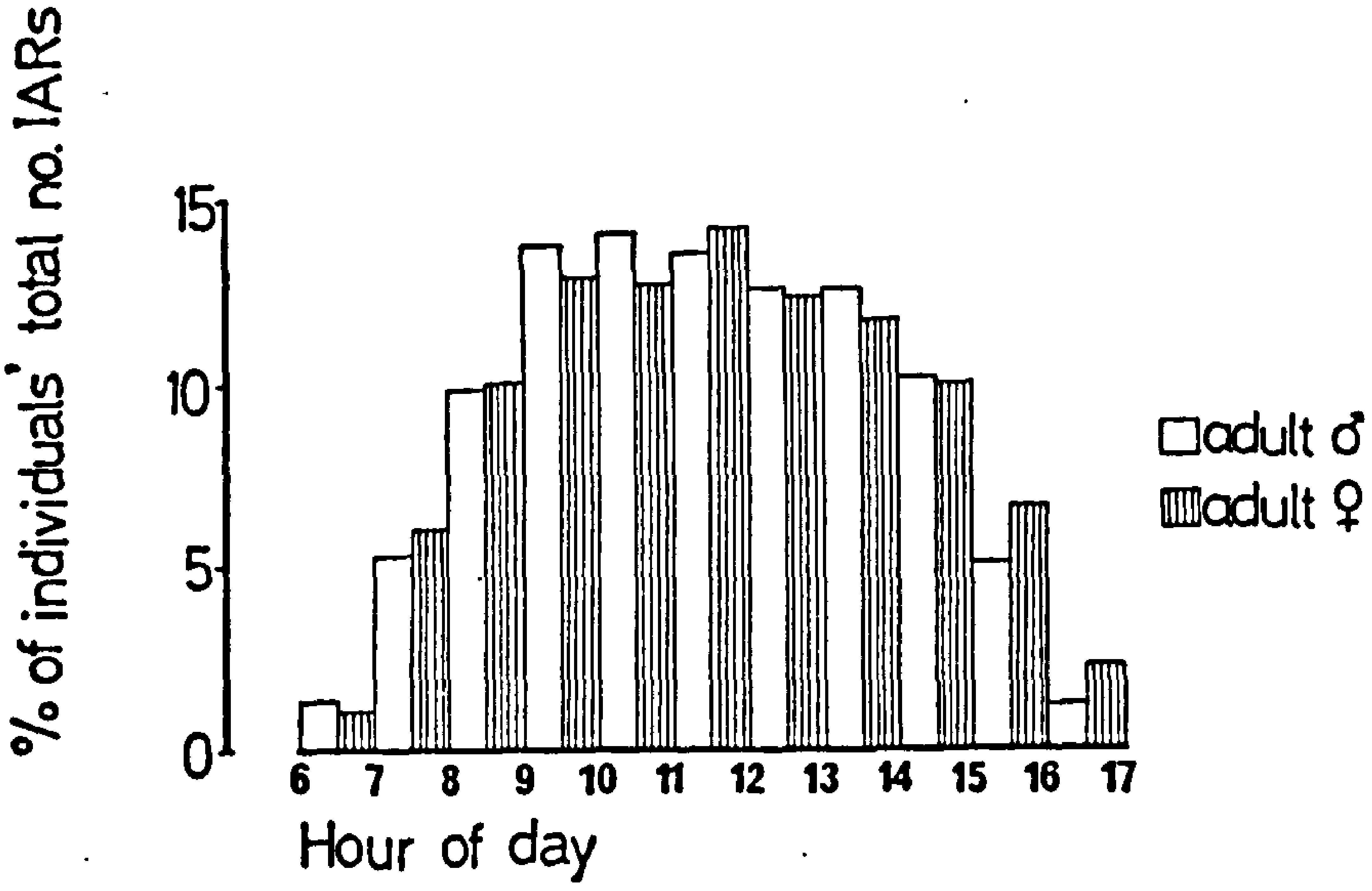
The distributions of individuals' IARs throughout the day did not vary (Figure2.7) greatly and were not sufficiently different to cause statistical problems or suspect a bias from seeing certain animals more often than others at certain times of the day.

The animals moved as a group around their home range and essentially performed the same activities at the same place simultaneously. However, for reasons associated

Figure 2.7 Hourly distribution of the proportion of each individual's Individual Activity Records (IARs) over the whole year in Group P and Group V.



GROUP P



GROUP V

with retaining contact with the group towards the end of their activity period, when they could be easily lost, the adult female of each group was most closely followed later in the day. In Group P this meant that the next morning this individual (and her dependent juvenile) would be adhered to until other members appeared and the day's top hierarchy member selected and subsequently followed. In Group V, mother-infant interactions at sleeping time were required to be seen.

9. SUMMARY

1. Approaches to the study of the behaviour and ecology of Indri had to be modified as a result of difficulties in finding and observing the animals. Three study areas, encompassing different degrees of disturbance of the forest and different forest types were selected. Two groups of Indri were habituated to the observer. A third group became gradually tame.

2. Indri were found to inhabit a dense, evergreen forest whose constituent plant species were poorly known. The ridged structure of the region contributed to a great local diversity in the size, shape and density of plant species.

3. Certain important biases were recognised in this study and attempts were made to construct a recording system that would firstly correct for them, and secondly remain stationary as the study progressed. Latitudinal point sampling was employed in regular observations of each group member's position and activity. Rarely occurring activities were continuously sampled and data on all vocalisationsheard from all groups were collected.

4. The representativeness and independence of the data were tested before comparisons were made between individuals, groups, times of year, etc.

5. Using the adopted system a large proportion of the

total amount of behaviour which could have been collected, was obtained. Approximately equal numbers of records were collected for each individual, for each hour of the day and for each Circuit. The efficiency of the sampling system was examined.

CHAPTER 3

Activity Patterns

The short period each day that *Indri* move around and feed is unusual for diurnal primates. Some weight is given in the following discussion, therefore, to factors which control the length of the activity period - some which may be environmental e.g. temperature, rainfall, daylength, and others which may be related to the presence of an infant. Differences between groups in the timing of their activity period may provide a source of variation that is useful in considering (and sometimes rejecting) the identity and nature of these influential factors.

1. A TYPICAL DAY

Indri sleep in trees 10 to 40 metres above the ground, resting on single wide horizontal boughs or at the junction of slimmer branches. The dispersion of the sleeping group is similar to that occurring during the active hours, animals being spread about an area of between a quarter and one half of a hectare. The mother and infant sleep in contact with each other. The latter, who at an early age is enclosed in the mother's folded body (sleeping posture), later clasps on behind in the 'locomotive' position (Jolly 1966), for the duration of the inactive period. Occasionally, when the weather is exceptionally wet and cold, other animals may form such aggregations, but no more than two individuals are ever involved (Plate 3.1).

Indri are strictly diurnal having a short activity

PLATE 3.1 Sleeping postures of *Indri indri* (Group P) at Analamazoatra. To the left the adult female is sleeping with the youngest offspring (01) clasped on behind in a sleeping 'locomotive'. To the right, the next youngest offspring, a sub-adult (02) sleeps alone. Normally this individual (02) slept further away from the adult female and 01.

period that varies seasonally in its timing and durations. Self-grooming or grooming the partner in a sleeping combination is the first activity to be seen and begins from between 2 to 4 hours after dawn, with no change in position or posture. Infants may suckle at this time, but normally moving and feeding, sometimes of the sleeping trees themselves, soon commences. All members of an Indri group become active over a period of 5-10 minutes.

A short feeding bout on plants in the immediate vicinity usually precedes individual progressions to a nearby spot where the animals meet, low in the forest, and defaecate simultaneously and close together. The morning defaecation session acts as a temporal reference point from which the individuals of a group may, having reassociated temporarily, choose to remain centrally involved in subsequent group movements or travel and feed on the group's periphery.

If fruit were plentiful the group would then usually make for a particular tree or group of trees in a major progression of up to 200 metres and feed together for up to 3 hours. Fruiting trees would often be found in small clusters and the animals would partially disperse and alternately visit neighbouring trees, or progress together to another fruit feeding area. If no fruit were available young leaves or leaf shoots would be selected, either from a similarly dense source or by successively visiting several dispersed trees, and consumed for a comparable period. From time to time small movements within food trees would bring two animals close to each other and one would then be aggressively displaced. Normally, however, the group spread themselves maximally about the trees.

At any time during the first half of the day's activity period the group might, spontaneously or in response to calls from another group, make loud wailing calls (song) for up to 4 minutes.

Another progression, feeding on young leaves, flowers, leaf buds and the occasional fruit would then commence, the group widely dispersed yet generally moving in one direction. Towards the middle of the afternoon, with the end of the active period approaching but with several hours of daylight remaining, Indri would characteristically move less frequently and feed less intensely. Grooming and scratching occurred shortly after or before a final resting position had been selected and the animals would rest and soon appear to sleep.

Within this general pattern there were seasonal variations according both to the phenological state of individual trees or species and to the duration of the activity period. During the austral summer when daylength is longest, for example, young animals would play together from time to time throughout the day.

Indri spend about one half of the activity period feeding. The rest of the time is devoted to short resting bouts and moving between food sources. There are no gross changes of activity during the period between first and last feeding/moving observations. Agonistic and affiliative interactions between group members are infrequent and occur only in short bouts.

2. THE DAILY ACTIVITY PERIOD

Indri are active from 5-11 daylit hours in a continuous rhythm. Variation in the timing and length of the active period, defined as the time between the first feeding observation and the last locomotor movement, is dependent on the weather, season, temperature and, probably, the reproductive state of the group. The categorisation of 'activity' is a discrete and natural one and may be precisely measured. Temporary changes in its duration are discussed below.

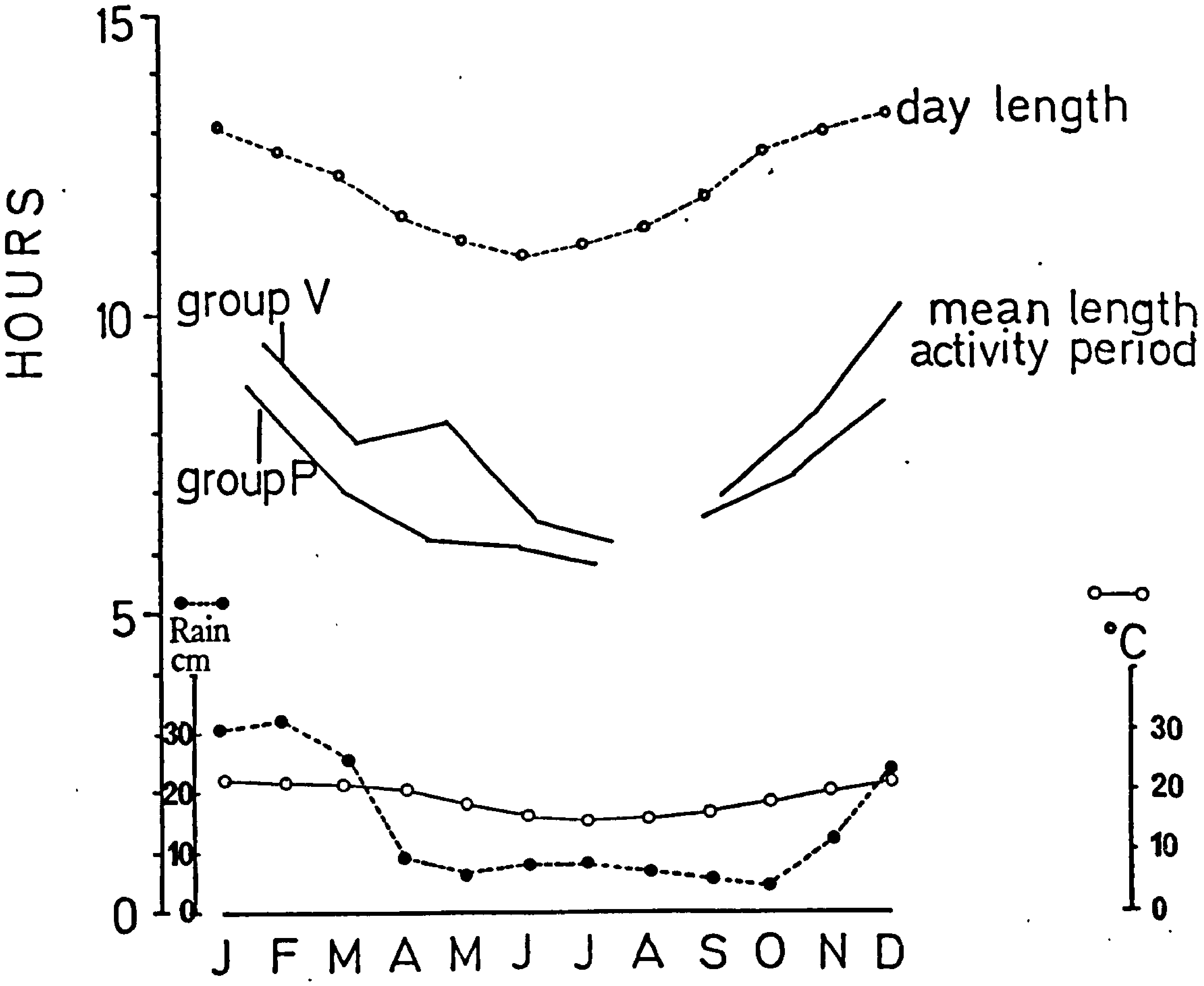
2.1. Seasonal Variation.

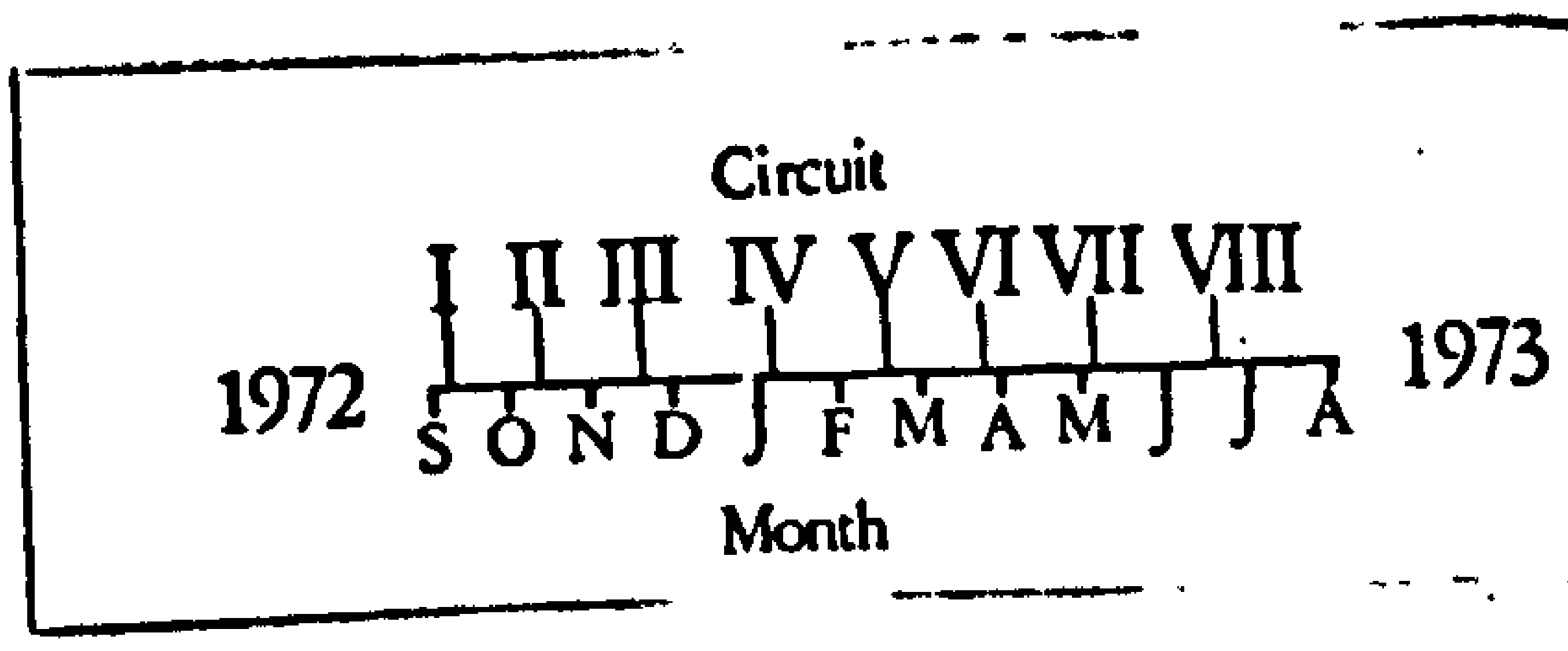
2.1.1. Daylength.

The southern location of the study areas, despite occupying tropical regions, resulted in seasonal variation in day length (Figure 3.1). Throughout the year *Indri* began and ended activity in broad daylight, several hours after dawn and before dusk. The rate at which the duration of the activity period changed seasonally was, however, faster than that of daylength, and other controlling factors are probably involved:

Activity period of:	GROUP P	GROUP V	DAYLENGTH	
Summer maximum	9.0	10.1	13.3	Hours
Winter maximum	5.8	6.1	10.9	Hours
DIFFERENCE	3.2	4.0	2.4	Hours

Figure 3.1 Seasonal variation in daylength, rainfall and mean temperature at Analamazoatra, with the mean duration of each study group's activity period.


HOURS
15
10
5
0
day length
group V
group P
mean length
activity period
Rain
cm
30
20
10
0
°C
30
20
10
0
J
F
M
A
M
J
J
A
S
O
N
D


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
1973
Month

2.1.2. Temperature.

Local thermometric records were not kept inside the forest because of the great vertical variability known to exist in such environments (Allee 1926, Allen et al 1972). Cold days appeared to delay the start of activity on some occasions but not on others. The cooling properties of the environment probably depend as much on humidity, air turbulence and precipitation as they do on the small variations in temperature between seasons.

Haddow (1952) claimed that rain does not penetrate the hydrophobic qualities of monkey fur and certainly most water appeared to be retained on the coat surface of Indri. This was frequently shaken off, however, and the increase in auto-grooming in wet weather was also suggestive of the unpleasant (cooling) properties of heavy rain.

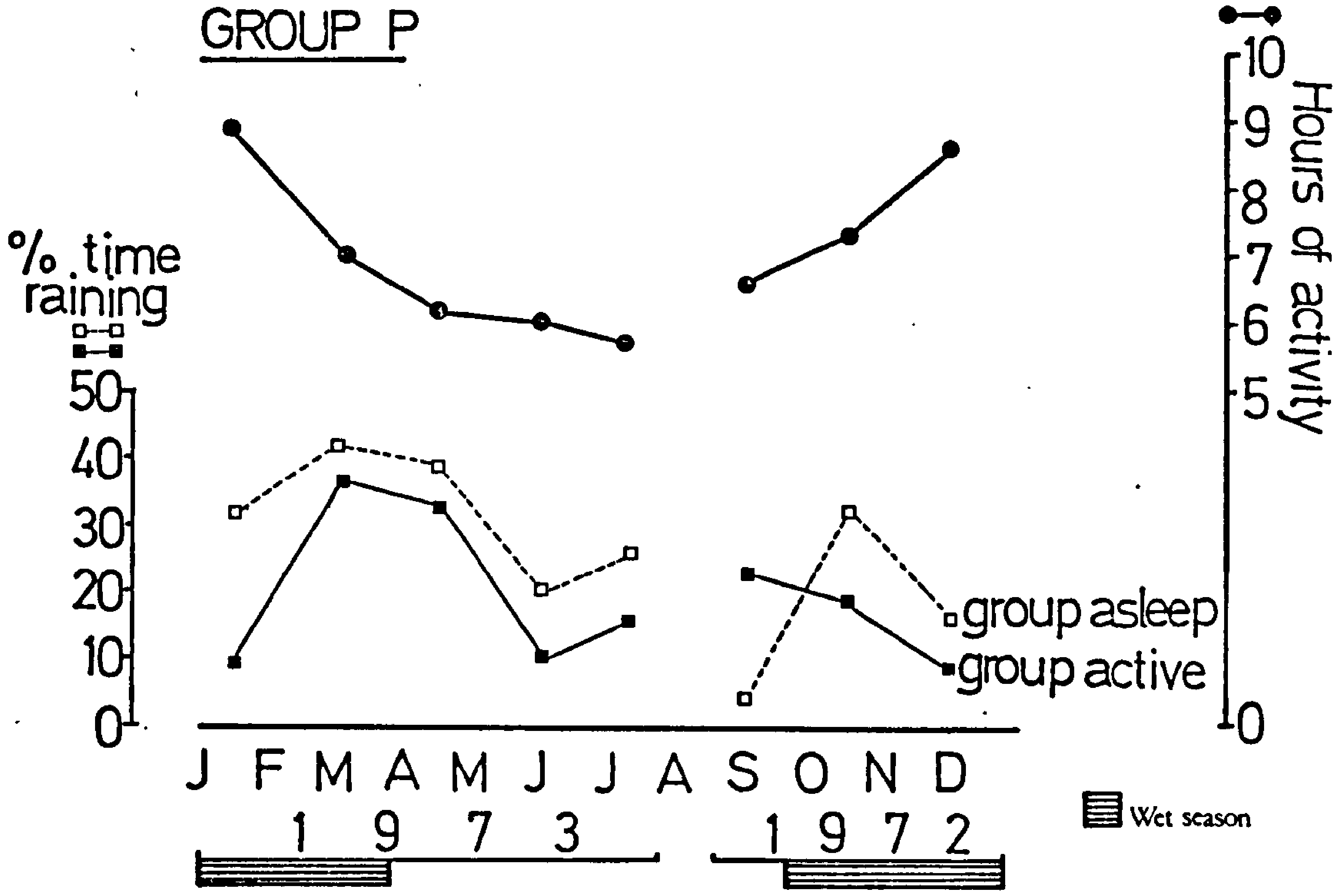
2.1.3. Rain.

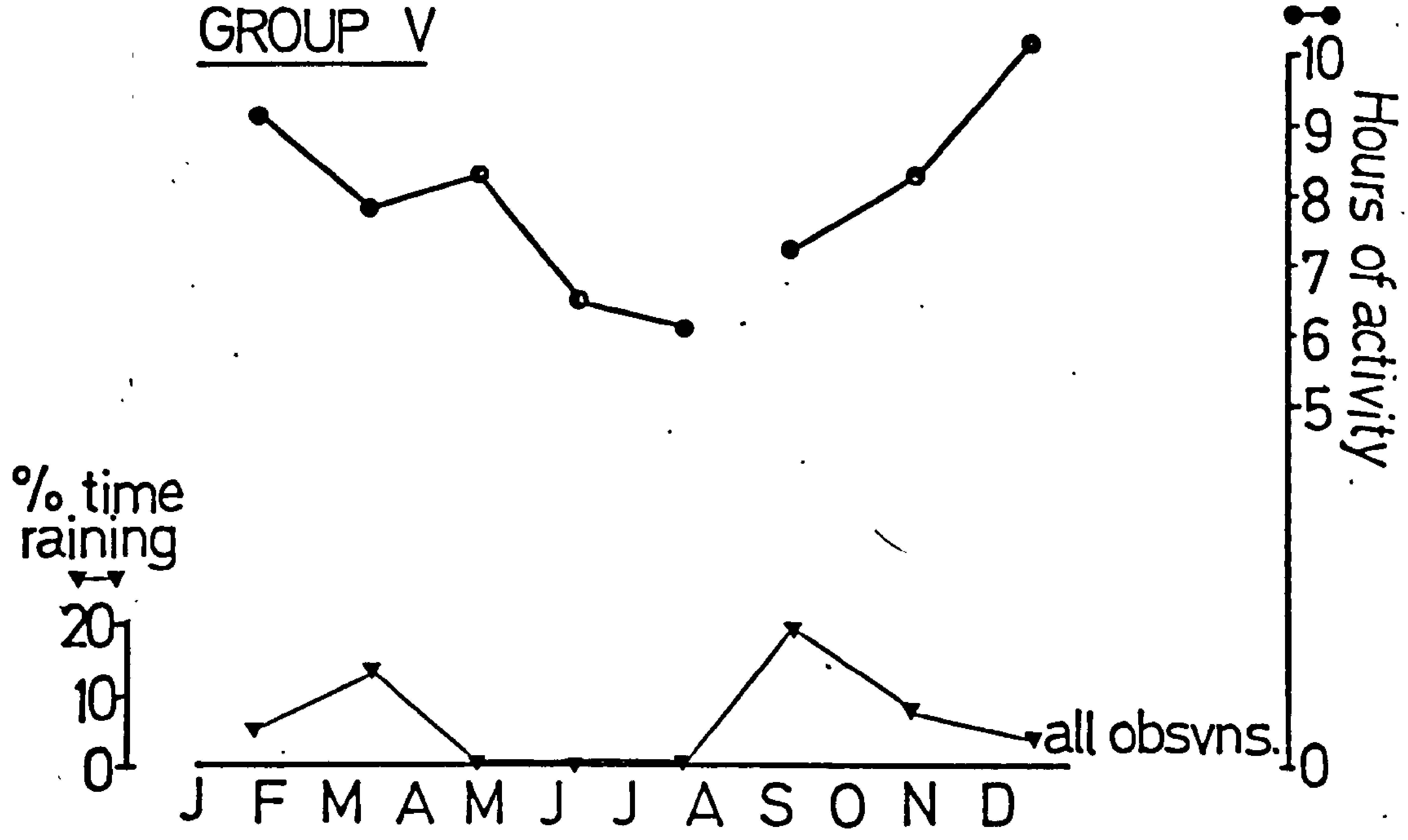
Rainfall alone did not account for seasonal variation in the duration of the activity period as (by chance) the proportion of time during which rain fell was not equal for the two study groups' observation periods (Figure 3.2). In neither group was the amount of time that rain fell per circuit negatively correlated with activity period duration. Throughout the year, however, more rain fell before and after than during the active periods of Group P.

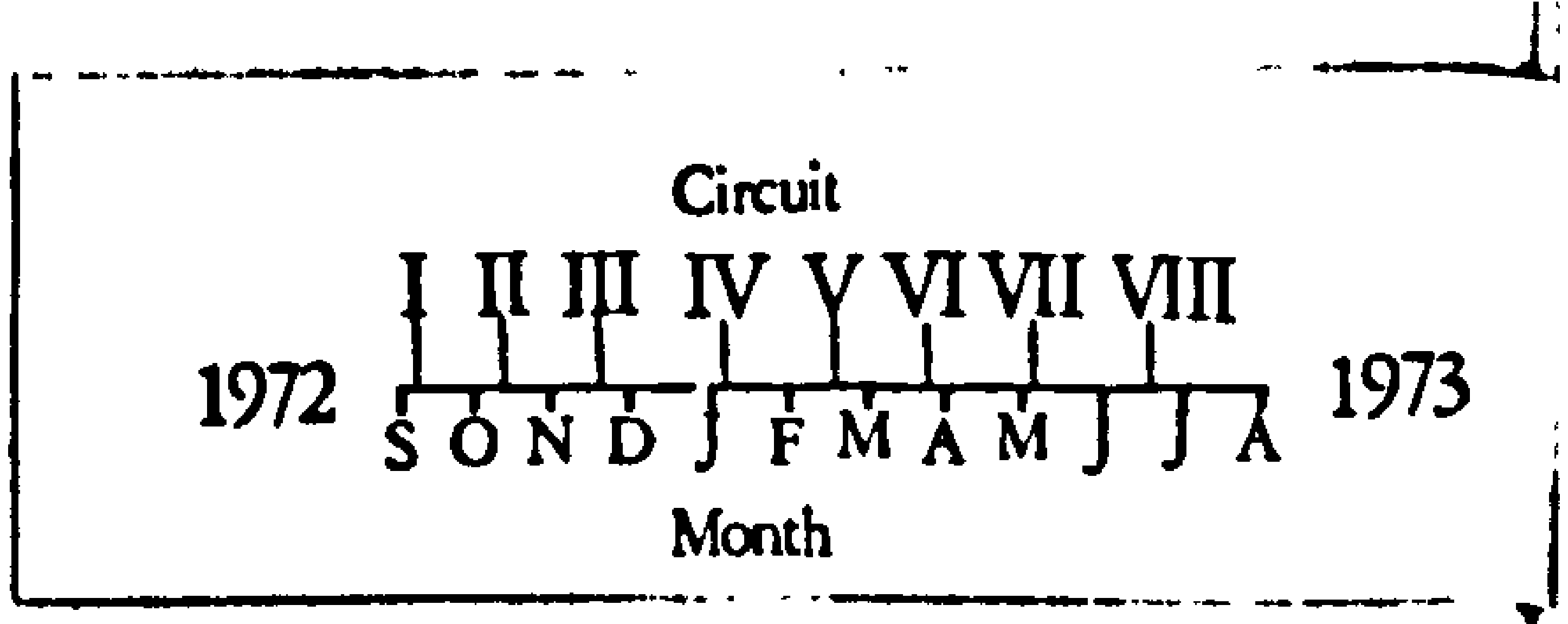
2.2. Daily variation in the duration of the activity period.

Only during observations on Group P was there sufficient variation in rainfall to examine its relationship

Figure 3.2 Seasonal variation in each group's activity period duration and the proportion of time that rain fell during each period of observations.


GROUP P
% time raining
50
40
30
20
10
0
group asleep
group active
Hours of activity
10
9
8
7
6
5
0
J F M A M J J A S O N D
1 9 7 3
1 9 7 2
Wet season


GROUP V
% time raining
20
10
0
all obsvns.
Hours of activity
10
9
8
7
6
5
0
J F M A M J J A S O N D


Circuit
I II III IV V VI VII VIII
1972
S O N D J F M A M J J A
1973
Month

with the activity period. The activity period was correlated in length with the proportion of time that no rain fell for 7 of the 8 Circuits but only in Circuits IV ($r^s = 0.754$, $0.001<p<0.01$) and VI ($r^s = 0.664$, $0.01<p<0.05$) were these correlations[1] significant.

The amount of time during which rain fell each day was positively correlated with the hour that activity ceased in all Circuits but significant only for Circuits IV ($r^s = 0.686$, $0.01<p<0.05$), V ($r^s = 0.648$, $0.01<p<0.05$) and VI ($r^s = 0.687$, $0.01<p<0.05$). The amount of subsequent daily rainfall was significantly negatively correlated with the hour of first activity only for Circuits IV ($r^s = -0.616$, $0.01<p<0.05$) and VIII ($r^s = -0.847$, $0.001<p<0.01$) - for other Circuits these measures had a correlation of approximately zero.

The amount of time that rain fell the previous day was not consistently or significantly correlated with the day's activity period duration.

The range of times of first and last activity were clearly too great to be accounted for only by variation in the proportion of time that rain fell and the degree of significance of the correlations presented above was not related to the overall amount of time that rain fell during the Circuit (Table3.1).

Beyond seasonal variation, those days in which activity began early in Group P were also often those days in which activity continued late (Figure3.3). This was especially true for Circuits II ($r^s = 0.88$, $0.001<p<0.01$) and IV ($r^s = 0.75$, $0.01<p<0.05$) for Group P.

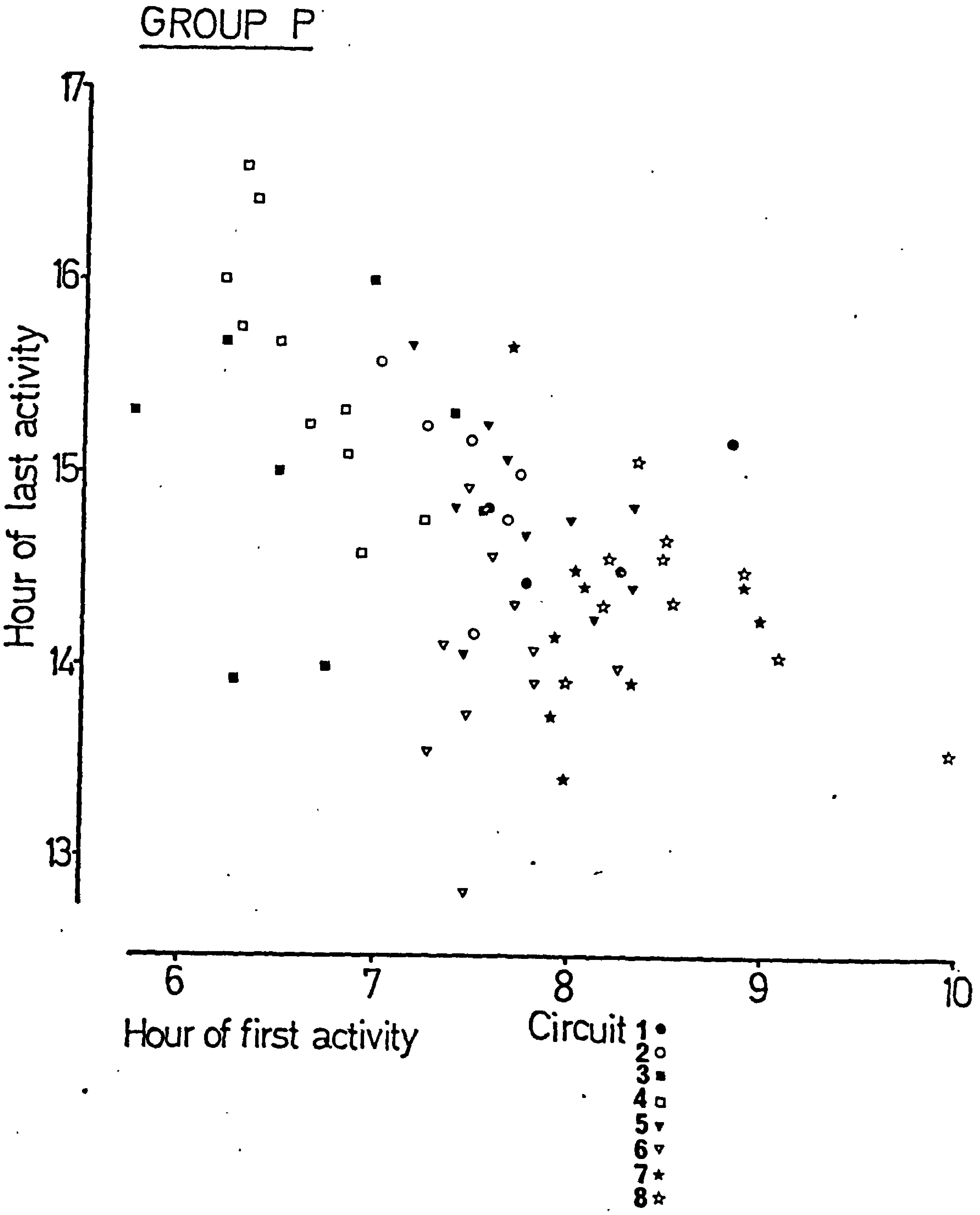
---

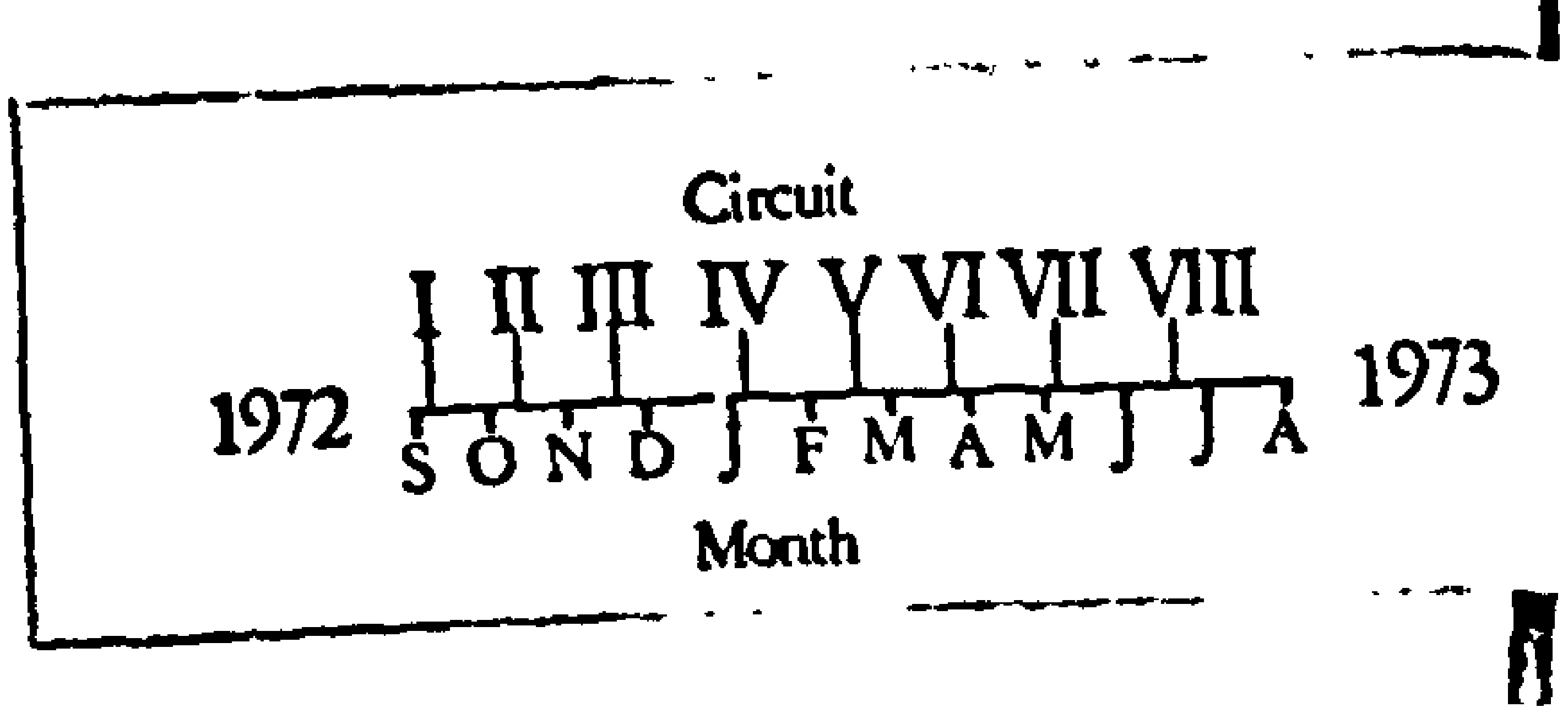
[1] Unless otherwise stated these are Spearman rank correlation coefficients, r^s.

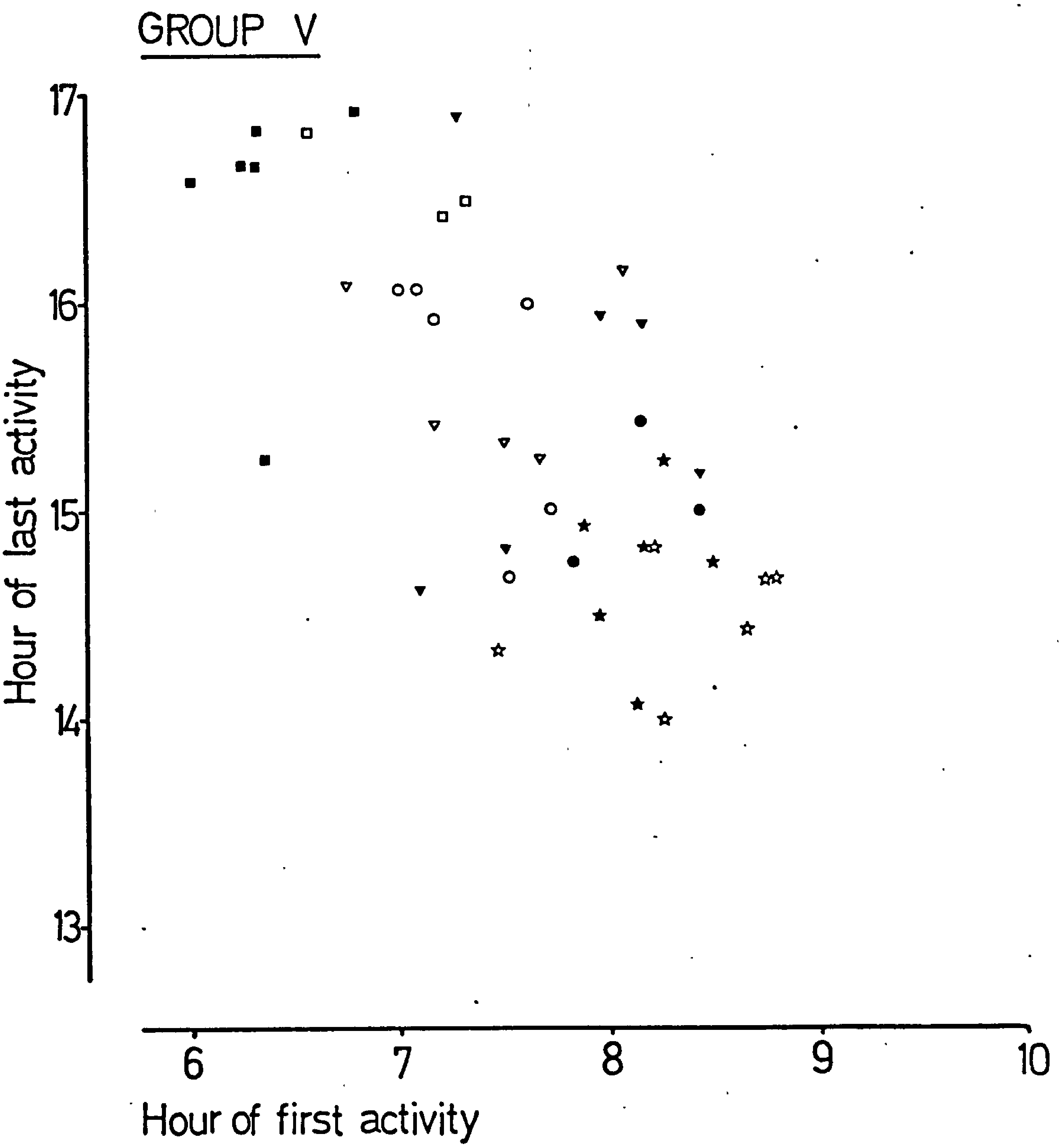
CIRCUIT	I	II	III	IV	V	VI	VII	VIII	X (mean)
% Rain P	16.7	22.2	7.5	12.5	35.6	34.8	16.0	18.9	20.5
% Rain V	19.4	8.0	4.2	5.8	13.9	0.5	0.0	0.5	6.5
Range P 1st Act.	74	79	109	63	70	59	78	120	81
Range P Last Act.	45	85	125	120	95	115	135	75	99

TABLE 3.1. The proportion of the activity period for each group during each Circuit that it was raining. The range in minutes of the timing of first and last activity each day are shown for Group P in each Circuit.

<u>Figure 3.3</u> The relative timing of first and last activity in Group P and Group V. Each point represents one observation day where the time of the first and last moving or feeding activity in each group were recorded.


GROUP P
Hour of last activity
17
16
15
14
13
Hour of first activity
6
7
8
9
10
Circuit 1 ●
2 ○
3 ■
4 □
5 ▼
6 ▽
7 ★
8 ☆


Circuit
I II III IV V VI VII VIII
1972
S O N D J F M A M J J A
1973
Month


GROUP V
Hour of last activity
17
16
15
14
13
6
7
8
9
10
Hour of first activity

No such relationship existed during the short periods of observation on Group V.

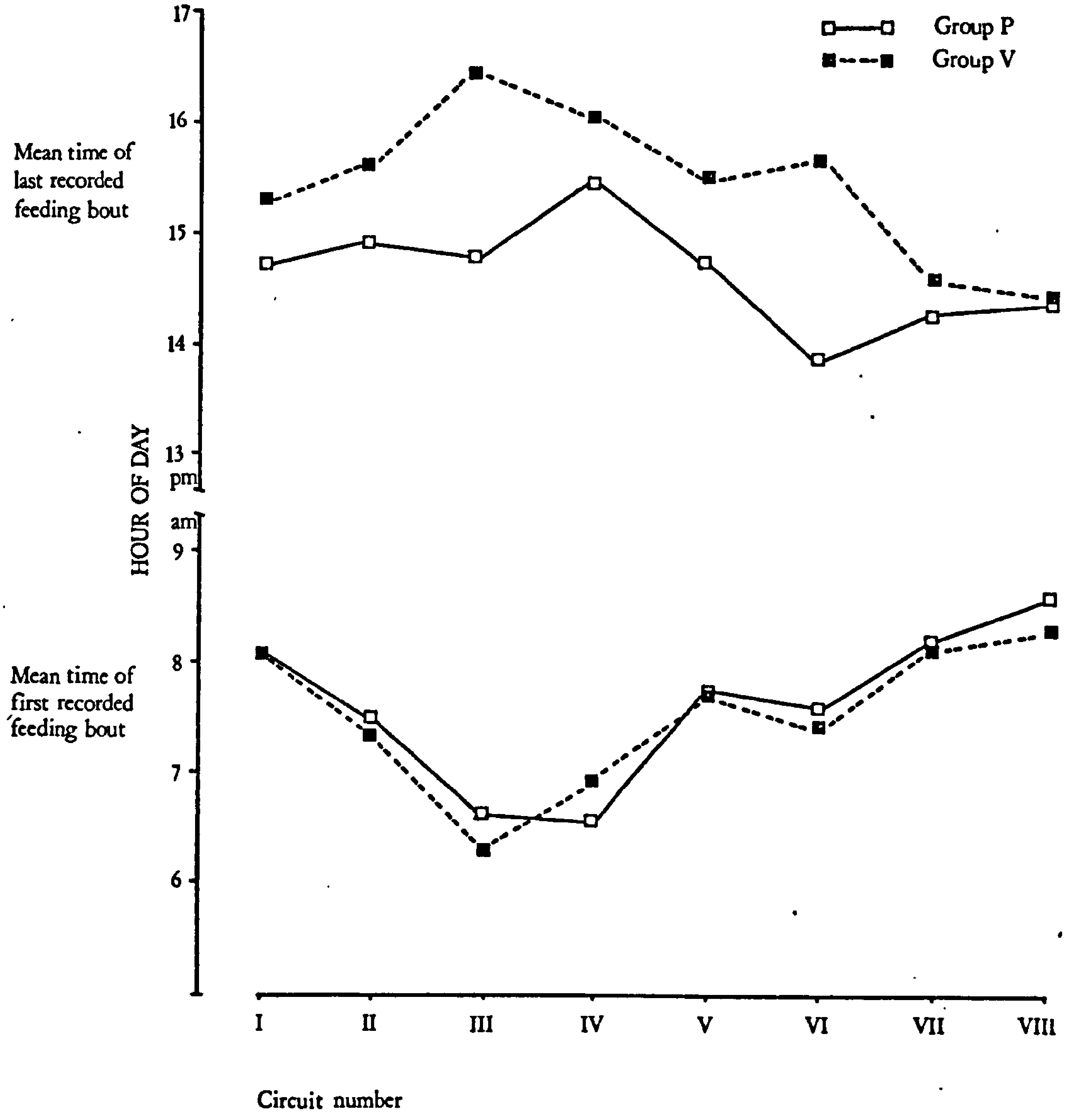
There were no correlations between the time that activity ceased and the time of first activity the following day.

From observations in all study areas the observer gained the impression that although daily variation in the timing of both first and last activity was great (see Fig.3.3), too great to make correlative generalisations, warmer, finer days tended to be associated with longer activity periods. The timing of rain may have been more important than the actual amount or duration. Hard rain at about the time that Indri normally became active would usually postpone feeding and moving and, if it fell towards the end of the activity period, would hasten the adoption of sleeping positions. In between even hard rain might be ignored, especially if it lasted for long periods, but short downpours would often cause Indri to take up solitary, huddled postures.

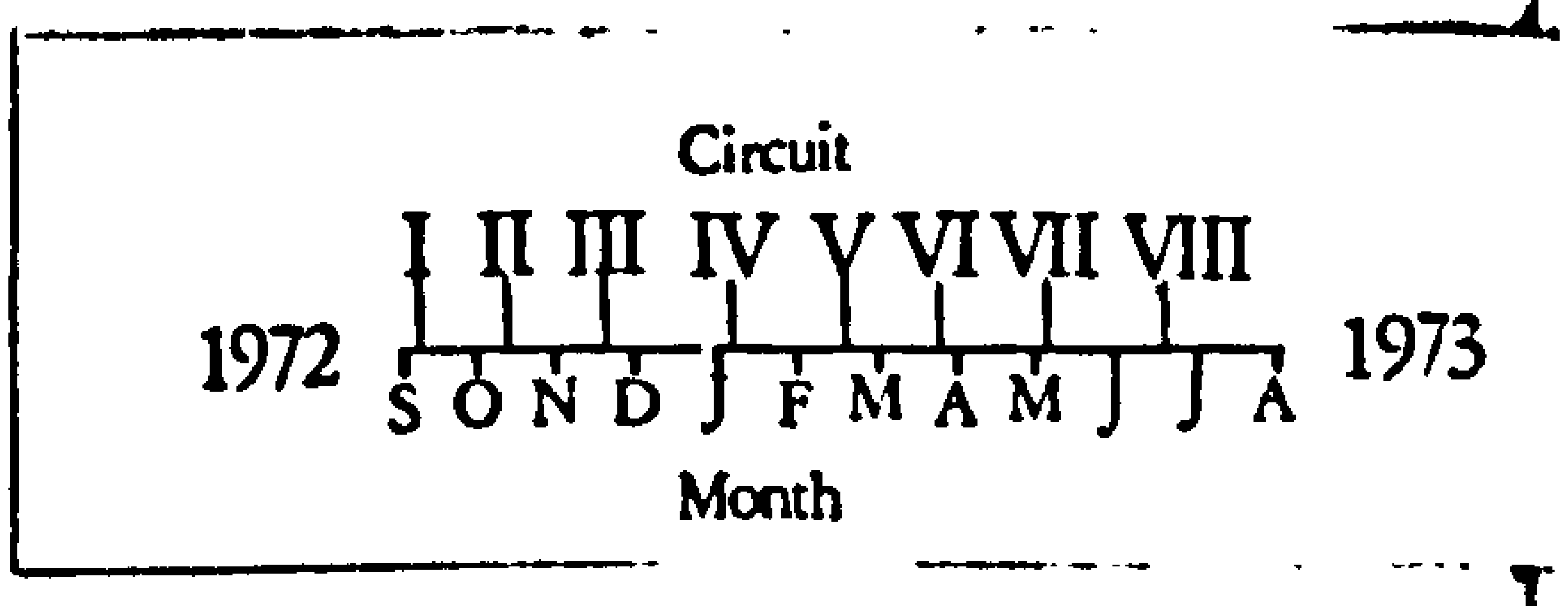
2.3. Inter-group variation in activity period duration.

The different durations of the adjacent study groups' activity periods (Figure3.4) could be attributed to the late afternoon extension of activity in Group V. Both groups became active at comparable times but Group V, until the last Circuit, consistently moved and fed after Group P had taken up sleeping positions (Table3.2). By the end of the study no differences in the timing or duration of the two study groups' activity periods were

Figure 3.4 Mean time of first and last recorded feeding bout for each study group in each Circuit.



Group P
Group V
Mean time of last recorded feeding bout
Mean time of first recorded feeding bout
HOUR OF DAY
17
16
15
14
13
pm
am
9
8
7
6
I
II
III
IV
V
VI
VII
VIII
Circuit number



Circuit
I II III IV V VI VII VIII
1972
S O N D J F M A M J J A
1973
Month

CIRCUIT	FIRST ACTIVITY			LAST ACTIVITY		
	U*	n1,n2	p	U*	n1,n2	p
I	11	6,5	0.27	4	6,5	0.026
II	28	8,6	>0.525	11	9,6	<0.05
III	31	8,6	>0.525	2	10,6	<0.001
IV**	10	10,4	>0.05	13	10,5	>0.05
V	32	10,6	>0.05	12	10,6	<0.05
VI	26	10,6	>0.05	0	10,6	<0.001
VII	25	9,6	>0.05	11	10,6	<0.025
VIII	22	10,6	>0.05	21	10,6	>0.05

Null Hypothesis: that Group V does not begin or retain activity later than Group P.

* Tests of significance based on the Mann Whitney U test.

** The results for Group V include data collected during a three-day cyclone.

TABLE 3.2. Differences in the timing of first and last activity between Group P and Group V during each Circuit.

apparent.

Only during Circuits II and III were there sufficient numbers of dry days whilst observing Group P to statistically compare activity period durations between groups under comparable weather conditions. As for both Circuit III (Mann Whitney 'U' test, $n_1=n_2=5$, U=0; p=0.004) and II (Mann Whitney 'U' test, $n_1=4$, $n_2=5$, U=1; p=0.016) the activity periods of Group V were superior in length to those of Group P, rainfall alone did not explain the differences.

The short activity periods of the 2 study groups of Indri compared to other diurnal primate species required confirmation from other Indri groups. These were, unfortunately, very difficult to obtain. Group IV at Vohidrazana were observed to take up sleeping positions at 1355 on 13 June 1972 and became active at 0858 the next day. On the 7 July the group slept from 1437. All other observations on both this and other Indri groups in all study areas were consistent with short, diurnal activity periods that finished early in the afternoon.

Surveys in all forests visited during the course of the study failed to locate Indri after 1500 whilst sympatric lemurs; Hapalemur griseus, Lemur fulvus fulvus and Propithecus diadema diadema being those most commonly encountered, were often seen to be active much later in the day (see Section 5.2). Furthermore, these species (especially Hapalemur) became active earlier.

2.4. Deviations from continuous daily activity patterns.

2.4.1. Quiet periods.

From time to time an *Indri* group would apparently spontaneously cease activity and rest quietly for periods of up to 2 hours. This was observed on at least 11 occasions (6 in Group P, 5 in Group V) in the two main study groups. It also commonly occurred when stalking unhabituated *Indri* who, when rigorously pursued or if they became aware of the observer only when he was very near, would remain immobile for long periods. Richard (1973) during the process of habituation of *Propithecus verreauxi* noted a similar response that lasted for almost ten hours. Eventually leaving the immobile animal Richard returned a little later to find it had disappeared. These observations are not only identical to those made on *Indri* but also the remaining genus of the family, *Avahi* (pers. obs.). Immobility is, apparently, a behavioural response to humans (and, perhaps, all potential predators) common to all Indriids and, maybe, all folivorous lemurs (Charles-Dominique & Hladik 1971).

On at least 3 of the instances in which these 'quiet periods' occurred in the study groups at Analamazoatra, there were noisy[1] birds (*Alectroneas madagascariensis*, *Leptosemus discolor* and some member of the indigenous family Vangidae) in the vicinity. All these birds are harmless to *Indri* in that they are non-predatory. However,

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[1] Bird vocalisations in these cases may have arisen from the presence of the observer.

in frequent observations, the two common rapaces, Polybiroides radiatus and Buteo brachypterus, whilst often evoking alarm calls from Indri, never attempted to attack or subsequently affected in any way the activity of the study animals. On one occasion I was myself attacked by a small bird of prey, probably Falco newtoni, presumably because it was nesting nearby, and this might prove a hazard to arboreal mammals as they forage and feed in canopies of the forest.

The presence of a dog appeared to cause immobility in Group V for 50 minutes on 24 October 1972 despite its immediate departure and its ignorance of the animals' whereabouts. Encounters with Propithecus diadema diadema (18/11/1972) and with other Indri (22/10/1972) also resulted in short periods of inactivity. Animals may, of course, have been perceived by Indri on other occasions whilst remaining hidden to the observer.

Interactions with other species, however, did not always result in 'quiet periods'. Frequent encounters between Indri and Lemur fulvus, for example, although sometimes momentarily causing Indri to stop feeding, were largely ignored.

On 7 occasions the time 'lost' during 'quiet periods' was greater than 40 minutes. On 3 of these the subsequent final activities occurred later than at any time that Circuit, but on the other 4 the active day ended normally. It was not apparent, therefore, that Indri made up time lost during these periods by extending the days' activities.

2.4.2. Suckling Periods.

Between Circuits II and VI inclusive, when the infant in Group V aged from 6 to 12 months, suckling could often be easily observed and sometimes persisted in bouts of up to 40 minutes. These occurred at any time of day and on reaching the final resting positions (Figure 3.5).

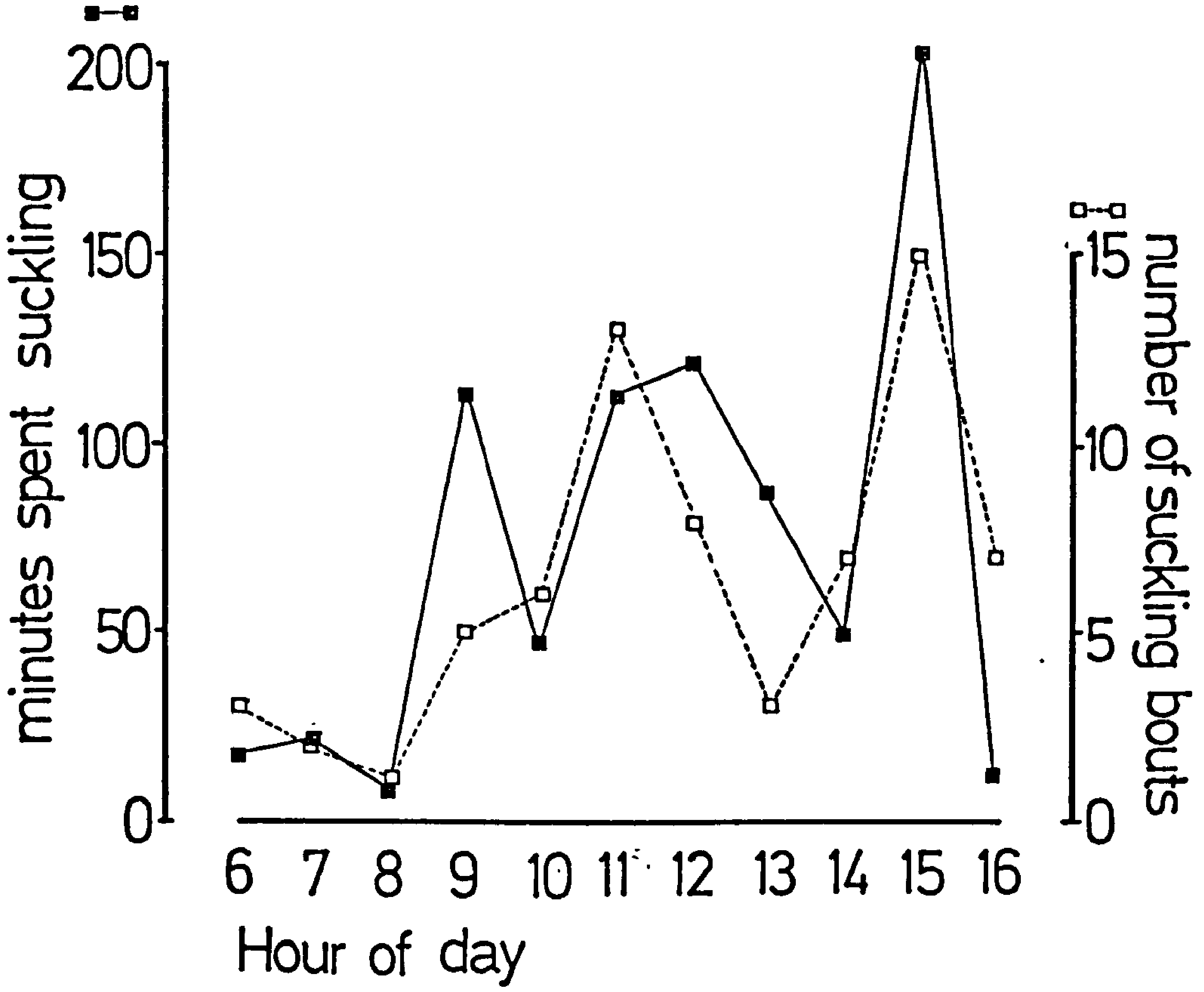
During a bout of suckling all activity within the group ceased and the Group V adult male rested until the infant had finished and the female had moved off to feed. The mean time spent by the infant in suckling each day varied from 6 to 53 minutes (Figure 3.6) and probably varied greatly between days (Chapter 10). These figures underestimate the true amount of time spent in this activity as intervening foliage sometimes interfered with the observations of suckling more than it did with obvious activities. Only during Circuits III and IV, when activity periods were at their longest, were considerable amounts of time 'lost' by feeding the infant (8.1% of the active day for Circuit III, 9.7% for Circuit IV).

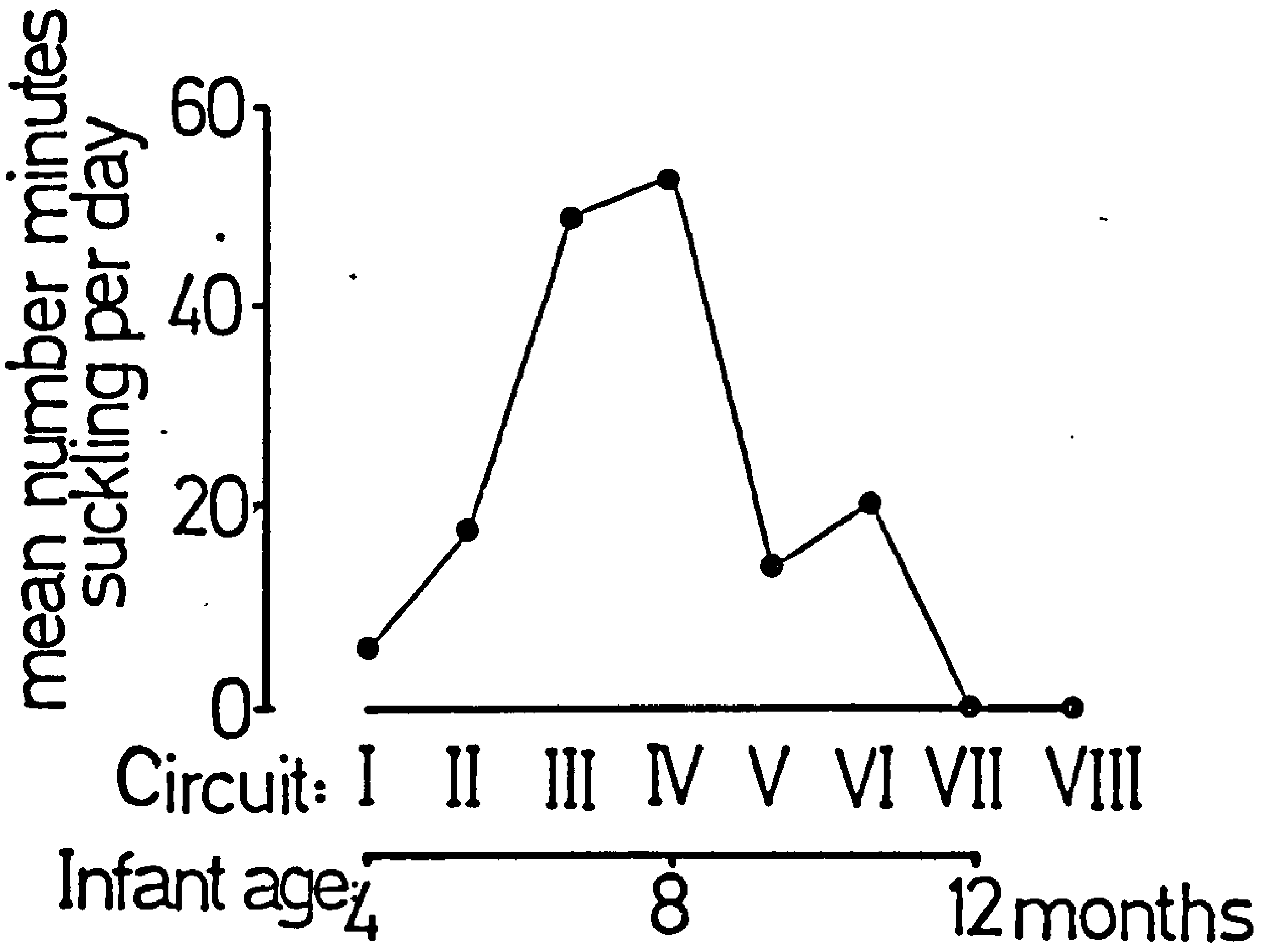
Only during Circuits III and V were there sufficient data to attempt correlations between the amount of time that suckling occurred and the duration of the activity periods. For both Circuits these proved non-significant (III: $r^s = 0.43$, $p>0.05$; IV: $r^s = 0.07$).

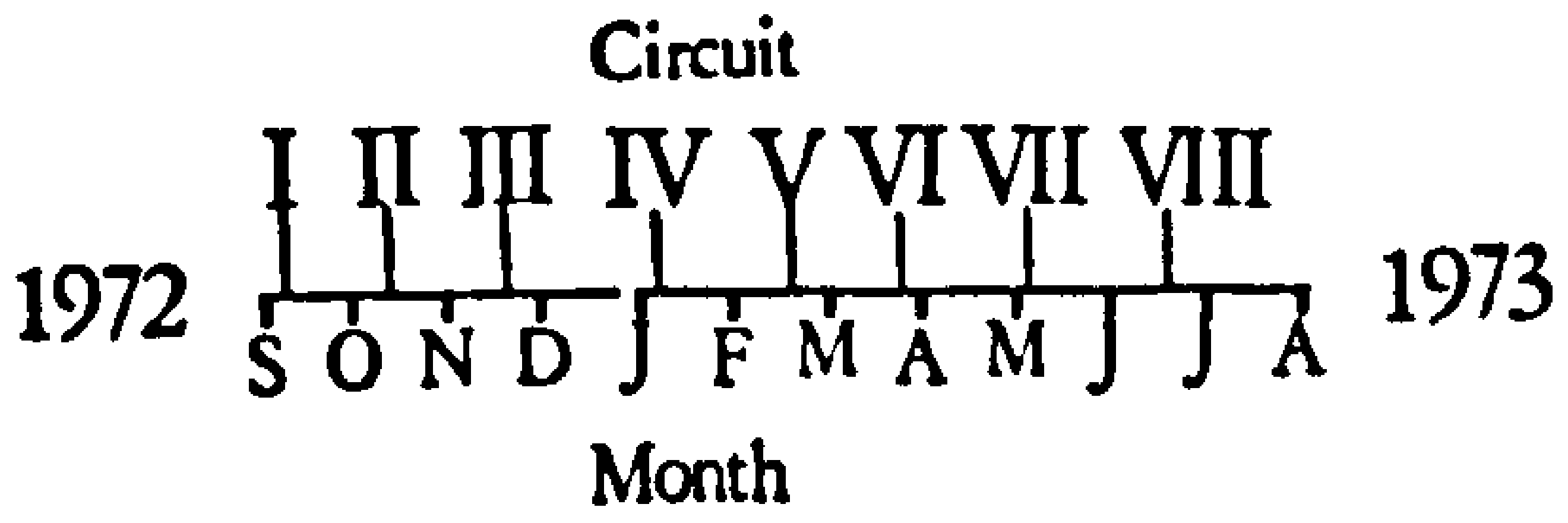
There is no reason therefore, to believe that <u>Indri</u> groups with infants extend their activity period to compensate for time spent suckling.

Figure 3.5 Hourly distribution of the number of suckling bouts and the number of minutes spent suckling throughout the year by the infant in Group V.

Figure 3.6 Seasonal variation in the mean number of minutes spent suckling per day by the infant in Group V.


minutes spent suckling
200
150
100
50
0
number of suckling bouts
15
10
5
0
6
7
8
9
10
11
12
13
14
15
16
Hour of day


mean number minutes suckling per day
60
40
20
0
Circuit:
I
II
III
IV
V
VI
VII
VIII
Infant age
4
8
12 months


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
1973
S
O
N
D
J
F
M
A
M
J
J
A
Month

3. SOCIAL ORGANISATION OF THE ACTIVITY PERIOD

Because group members became active over a very short period of time it is likely that social factors were influential in the regulation of activity initiation. Identical reactions within the groups to small changes in environmental conditions could conceivably account for the synchrony of first activity each day. The short spread of time (2-10 mins) separating the first movement of the earliest and latest group member suggests, however, that this is unlikely.

In Group P group members were too widely dispersed for the observer to be sure at any time of the presence or absence of specific forms of communication between animals at or just before the onset of daily activity. Usually only 1 or 2 individuals could be seen before activity commenced. As no specific sign or vocalisation was emitted at this time social control appeared to be directed by one (or some) individual(s) in the form of the first movement itself. The Indri group became active, therefore, when the first individual moved and began to feed. Only in Group V could data on the first animal to move be collected.

(a) Group V

Over the whole year (48 days) on 38 occasions (79.2%) the identity of the individual first to move from a sleeping position was recorded. The adult male moved first on 22 (58%) of the days and the adult female on 14 (37%). This difference was not significant

(X^2 test (1df) = 1.77, $0.1<p<0.2$). On 2 occasions the infant was first to move.

It is impossible to claim that individuals feeding last in a group postponed the termination of activity any more than those who first took up sleeping positions promoted it. On the 28 days that the last feeding observations could be ascribed to specific individuals, 9 were of the adult male (32%), 8 the adult female (29%) and 11 the infant (39%). The adult male was not seen proportionately less at these times than at other times of the day (Chapter 2) and it is unlikely that the percentage of occasions that the individual feeding last could not be identified (41.7%) contained relatively more of his feeding records (see Chapter 6).

(b) Group P

In Group P the proportion of records obtained at the first observation of feeding each day that each individual was seen feeding varied (between individuals) from only 55.7% to 68.1% and did not significantly differ ($X^2_{4df} = 0.2728$, $p>0.99$). No individual fed more often than expected (from their overall proportion of time spent feeding) during the first observations of feeding each day (5 X^2 tests $_{(1df)}$: Adult female $X^2 = 1.8236$, $0.1<p<0.2$; Adult male $X^2 = 1.9316$, $0.1<p<0.2$; O3 $X^2 = 2.838$, $0.05<p<0.1$; O2 $X^2 = 0.2705$, $0.5<p<0.7$; O1 $X^2 = 0.7603$, $0.3<p<0.5$).

Neither could individual differences in the proportion of last feeding observations explain the control of activity termination in Group P ($X^2_{(4df)} = 1.2286$, $0.8<p<0.9$).

Again the proportion of each individual's feeding records that coincided with the last feeding observations in the group, did not differ from their normal feeding behaviour (5 X^2 tests $_{(1df)}$: Adult female $X^2 = 0.0393$, $0.8<p<0.9$; Adult male $X^2 = 0.3517$, $0.5<p<0.7$; 03 $X^2 = 2.6913$, $0.1<p<0.2$; 02 $X^2 = 3.6908$, $0.05<p<0.1$; 01 $X^2 = 1.0826$, $0.2<p<0.3$).

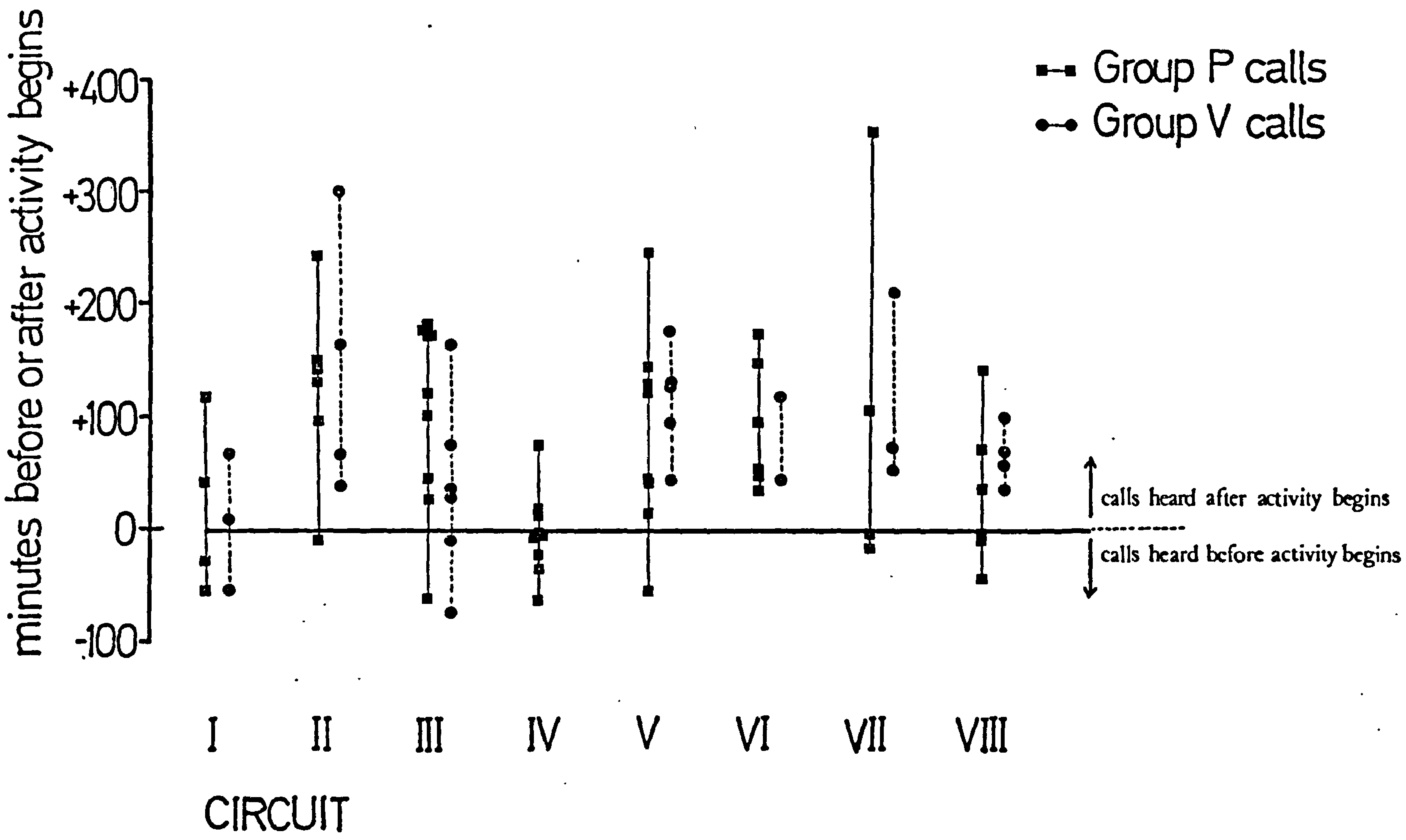
The control of activity period cannot, therefore, be attributed to particular individuals in either study group. It appears that extrinsic factors influence individuals slightly differently and cause any individual to become active or cease activity first. Others then very rapidly follow so as to maintain group cohesion. It may be that competitive elements of Indri behaviour are mitigated by this social synchrony or it may be that in so doing the group best remains geographically associated.

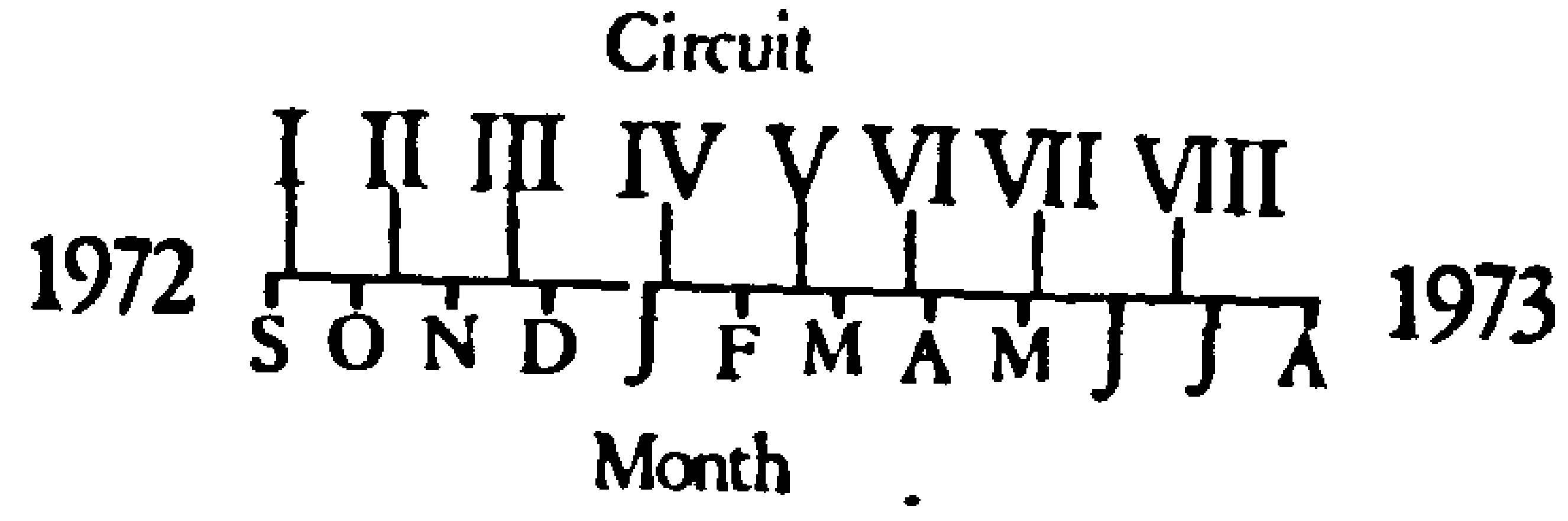
4. THE ACTIVITY OF THE POPULATION

Despite repeated observations on two study groups it was considered desirable to examine the activity of other Indri groups in the population. A comparison was therefore made of the relationship between the timing of the first 'morning calls' of the study groups and their first activity. A close or consistent relationship might be reasonably assumed to hold for other groups.

The results (Figure 3.7) show that this approach suffers from the excessive variability in the time of first calls. It appears that during Circuit IV, when the

Figure 3.7 The timing of each of the study group's first calls relative to the time of first activity. For each Circuit each spot represents the number of minutes after or before the first call by the group that they become active.


Group P calls
Group V calls
minutes before or after activity begins
+400
+300
+200
+100
0
-100
calls heard after activity begins
calls heard before activity begins
I
II
III
IV
V
VI
VII
VIII
CIRCUIT


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
1973
Month

vocal activity of the population was high (see Chapter 9), the time of the first call related more closely to the beginning of activity than at other times of the year. Calls emitted before activity began occurred on 29% of the days in Group P but only 11% of the days in Group V. This may have been due to the cyclone which interrupted observations on Group V during Circuit IV. Omitting this Circuit's data from both groups reveals no differences between groups ($X^2_{(1df)} = 0.9922$, $0.3<p<0.5$).

It is concluded that the timing of calls in the population could not be profitably used to determine other groups' activity patterns. Calling occurred mostly during the morning and could not, in any case, provide information on the hour at which activity ceased.

5. DISCUSSION

5.1. Primate activity patterns.

Unlike *Indri*, who feed and move throughout the day (see Chapters 6 and 7) most diurnal tropical mammals and birds have bimodal activity patterns. Feeding and moving, in addition to social activities, are found to occur predominantly during the first and last parts of the day, with mid-day resting periods encompassing the hottest hours. This pattern of activity is also typical of primates such as *Cercopithecus ascanius* (Haddow 1952), *Erythrocebus patas* (Hall 1965), *Gorilla gorilla berengei* (Schaller 1963), *Pan troglodytes* (van Lawick-Goodall 1968), to name but a few. Haddow (1952) notes that "all East African monkeys with the exception of *Papio* have two active periods in the day ...", one in the early morning and the other during the afternoon and evening. Baboons (Papio cynocephalus) at Amboseli forage and feed continuously but engage in social activities predominantly during the early and late hours (Altmann & Altmann 1970).

This pattern is not without exceptions. The insectivorous primates on Barro Colorado feed continuously (Hladik & Hladik 1969) and Colobus badius have single midday or multiple feeding peaks at Gombe Stream Reserve (Clutton-Brock 1972). Chivers (1969) found that changes in the atmospheric conditions hid an underlying two-peak daily feeding pattern in Alouatta palliata. A similar variability was found in seasonal comparisons of the activity of Cercopithecus mitis (Aldrich-Blake 1970). A seasonal and regional variation was found by Richard (1973) in the activity of Propithecus verreauxi. The northern subspecies (P.v. coquereli) retained a two-peak feeding pattern throughout the year whilst those of the south (P.v. verreauxi) abandoned it during the shorter active periods of the cooler, dry season. Other studies on Malagasy lemurs have not observed the same animals throughout the year.

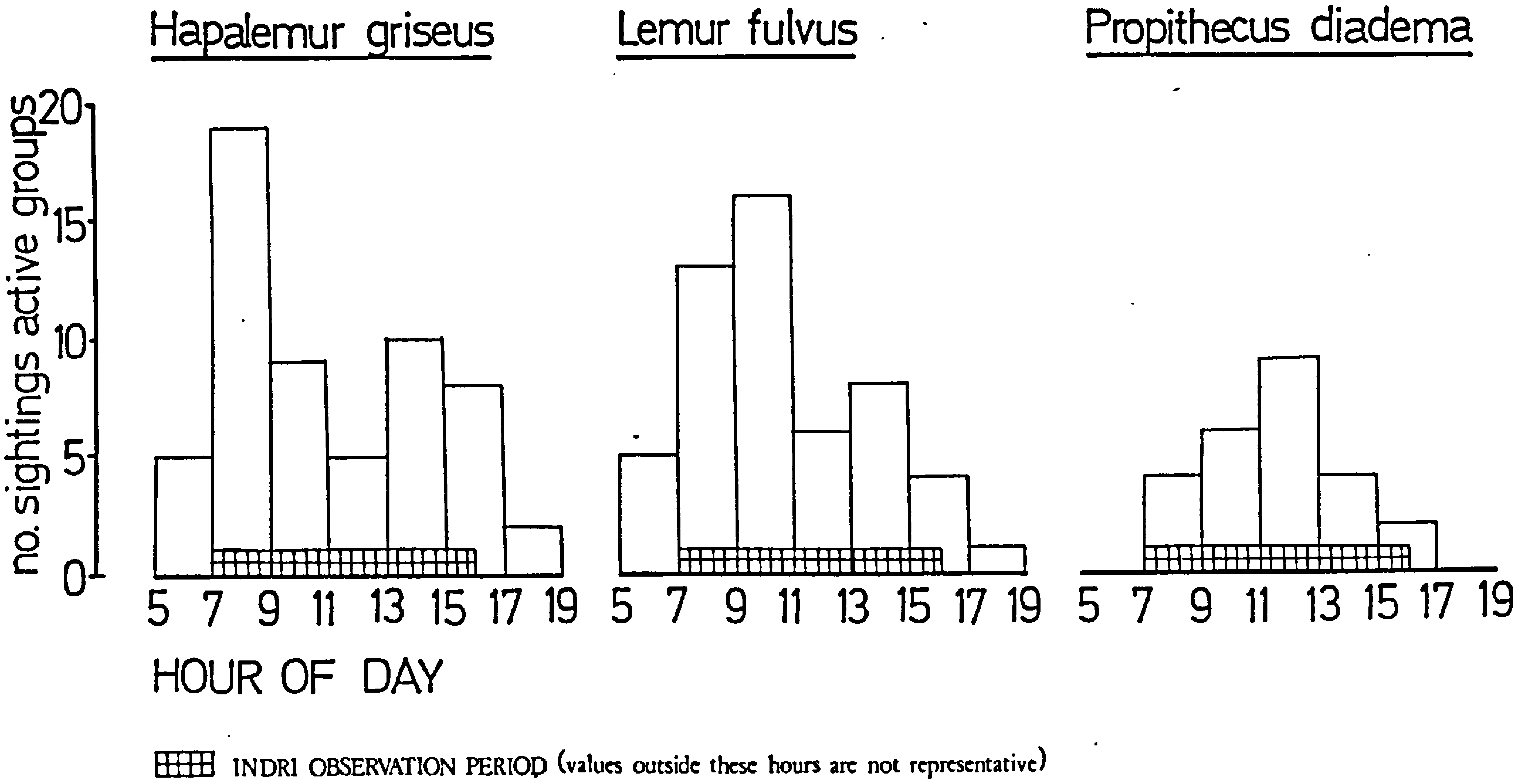
5.2. The activity of prosimians.

With the notable exception of the platyrhine Aotus, nocturnal activity within the order is confined to the Prosimii where it is predominant. All African and Asian strepsirhines are nocturnal and it is likely that this is a primitive characteristic (Charles-Dominique & Martin

1970, Charles-Dominique 1972, Martin 1972a, 1972b). If this is the case diurnality has evolved within the sub-order only in the Malagasy lemurs. Despite the vast morphological and behavioural radiation of the lemurs in Madagascar, nocturnality remains the dominant activity pattern. Of the twenty extant species only two (Indri indri and Propithecus verreauxi) can be claimed to be active only during the daylight hours and one of these (Propithecus verreauxi) feeds and moves late in the summer evenings when there is insufficient light for human observations (Richard 1973).

In contrast all the Cheirogaleinae are active only at night. Lepilemur and Daubentonia are also strictly nocturnal. The genus Lemur appears to be as variable in this characteristic as it is in many other aspects of behaviour (Martin 1972b), and although all the species are active at some time during the day, they may also feed and move at night (Jolly 1966; Tattersall & Sussman 1975b, pers. obs.). Hapalemur griseus of the west are reported to be crepuscular (Petter 1962, Petter & Peyrieras 1970a) and this activity pattern can be confirmed for those of the eastern rain forest (pers. obs.). Figure 3.8 shows the hour of sightings of lemurs sympatric with Indri where there were sufficient numbers of observations. Both Hapalemur and Lemur fulvus were seen less at about midday than at any other time and the latter were observed in social sleeping aggregations at 1255 (15/10/1972), 1250 (15/2/1973) and 1045 (9/7(1973) and 1130 (13/7(1973). Nocturnal activity in L.fulvus was

Figure 3.8 Hourly distributions of sightings of three lemur species sympatric with *Indri*, throughout the year.


Hapalemur griseus
Lemur fulvus
Propithecus diadema
no. sightings active groups
0
5
10
15
20
5
7
9
11
13
15
17
19
HOUR OF DAY
INDRI OBSERVATION PERIOD (values outside these hours are not representative)

marked at Analamazoatra[1] and had been previously observed in L.f.rufus in the west (Sussman pers. comm.). Lemur fulvus albifrons were seen feeding at night in August 1972 in the Reserve No.1. at Betampona near the coastal town of Tamatave.

Propithecus diadema diadema (Fig.3.8) are probably active throughout the day and possibly possess, like Indri, an approximately continuous activity pattern. From the 21 occasions they were seen, however, it is possible to say that they remain active much later than Indri for at least some of the year.

There is some evidence that nocturnal prosimians have two peaks of activity at night. This was clearly shown for Galago demidovii (Charles-Dominique 1971) and for at least part of the year by Lepilemur mustelinus leucopus (Charles-Dominique & Hladik 1971). Martin (pers. comm.) suggests a similar pattern for the activity of Microcebus murinus.

Although it is likely that there exist perhaps major seasonal differences, each lemur sub-family contains fundamentally nocturnal forms. Only the Indriinae

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[1] It was unclear what exactly L.fulvus were doing at night at Analamazoatra. They were frequently found making their characteristic calls and on most occasions 2 distinct groups were seen rapidly moving apart, as though they had been engaging in an inter-group encounter. Repeated observations of this behaviour at a specific spot suggested that this was associated with the border of a home-range or territory. On one occasion, however, a group was found calling whilst fleeing from a small arboreal carnivore, probably Galidicticus (Albignac pers. comm.).

possesses species fully specialised in diurnality and Indri is probably unique in its short daily activity. Unlike other diurnal lemurs, both of the west and the east, Indri (and possibly P. diadema) do not split up their active period into two or more divisions each day.

5.3. The control of activity in Indri.

As all animals were apparently in perfect health there was no reason to consider their maintenance activities inadequate. Sufficient time during their activity period was available to Group P for feeding and ranging etc. without having to extend their activities late into the afternoon like Group V.

Differences in feeding and ranging behaviour are fully described in Chapters 6 and 7 but a brief summary may be relevant here:

(i) The Group V adult female fed much more and had priority of access over food compared to the adult male.

(ii) The Group V adult female fed more than her Group P counterpart and, indeed all other animals in the study groups, for most of the year.

(iii) Group P moved in straight lines or wide arcs about their territory whereas Group V made more angled movements and moved to new trees more frequently.

Indri spend very little time in activities other than feeding and moving to new food sources and differences in activity period may be reasonably assumed to relate to feeding behaviour. The foraging-like movements of Group V

19

and the little feeding by the dominated male suggested either that there was a shortage of food in their territory, or, that there was less food available to the animals due to difficulties in locating and obtaining food. From observations on the position of food items in the forest itself the second explanation is favoured (see Chapter 6).Despite this, the Group V adult female was able to feed proportionately for the same amount of time as her Group P counterpart and, by extending the activity period, in real time achieved 10% additional feeding records.

Differences in weather and interruptions for suckling, it has been suggested above, do not account for the two groups' different activity period durations. There is some evidence that adult females lead *Indri* groups after the birth of an infant, thus selecting their choice of food as well as exhibiting social priority over it (see Chapter 7). When the infant started to feed in earnest both the differences between the adult male and adult female's time spent feeding, and the differences between the groups' activity periods reduced considerably (see Fig.3.4 , Chapter 10). This suggests that the Group V adult female effectively controlled activity period duration because she required considerably greater amounts of food to nourish the suckling infant.

There are few data on feeding behaviour in wild pregnant or lactating mammals. From parturition to weaning mammals may not be able to balance food intake with requirements (Sadleir 1969). The Pinnepedia, which copiously produce a richly nutritious milk over short periods of time, cease feeding altogether and rely on body reserves which are restored during the non-reproductive season. Many domestic or captive mammals, however, actively increase food intake during the period of lactation. Laboratory rats require 279 Calories during the 22 day lactation period compared to 79 Calories during the 22 day gestation (Sadleir 1969). Kaczmarski (1966) obtained similar results for the bank vole *Clethrionomys glareolus*.

It seems plausible to suggest that Group V remained active longer in order that the female, who might have had difficulties finding food, obtained sufficient nutrients to produce an adequate milk supply (see Chapter 6). Primates with generalised or partially carnivorous diets may be expected to alter their dietary habits so as to spend proportionately more time feeding on suitable foods. Folivore/frugivores whose intake of protein depends essentially on young foliage (Hladik et al. 1971) may only be able to accumulate sufficient nutrients through *increased* rather than *selective* consumption and therefore require more time to be spent feeding. It is likely (see Chapter 6) that both adaptations occurred in the behaviour of the Group V adult female whilst she was lactating.

5.4. Thermoregulation, photoperiod and the control of activity period in primates.

Mammals have imperfect temperature regulating mechanisms. By comparing the internal temperatures of Pro-, Meta- and Eutherian mammals with that of the environment, Martin (1902) suggested that primitive mammals regulated body temperature by heat production, enabling them to inhabit cold environments. Subsequent evolution of heat dissipation controls permitted warm environments to be exploited and made the maintenance of body temperature independent of activity (Scholander et al 1950a,1950b).

Gross changes in the activity of some Eutheria (hibernation, aestivation), when body temperatures approach those of the environment, are common. The evolution of seasonal changes in torpidity remains a controversial topic (Cade 1964, Hudson 1967) and there have been several suggestions that links with homeothermy may be tenuous. There is, in any case, great variation in the conditions inducing mammalian torpidity, the physiological and behavioural changes accompanying it and the factors controlling it (Johansen 1962, Pengelly 1967, Hudson 1967, Van Gelder 1971). Generally animals are obese before a period of torpor and reduce the load on their energy requirements by lowering body temperature, choosing a heat conserving environment such as a nest, hole or burrow, and slowing their metabolism. Within the dormancy period the activities performed by different species may vary considerably. Brown bears, for example, are conscious, may move about and undergo parturition and lactation in this state (Rausch 1961). Bats drink and urinate but do not feed whilst hibernating and many small mammals living in cold environments (e.g. Myoxus, Arctomys and Erinaceus) remain almost continuously asleep for long periods.

Daily changes in torpor are not restricted to non-mammalian species. Shallow, cyclical daily torpor, in which the body temperature drops considerably, occurs in the birch mouse (Johansen & Krog 1959), hummingbirds (Lasiewesti 1964), and bats (Hock 1951). Some insectivorous bats are only able to regulate their body temperature with some difficulty and are unable to fly after sleeping (when they have a low body temperature) without lengthy 'warming up' movements and shivering (Young 1957).

Hudson (1967) suggests that the ecological significance of daily torpor lies in its energy conserving properties at times when food is scarce. A graded rather than discontinuous distinction between seasonal torpidity and daily changes in activity may, therefore, be present in many mammals and mediated through incomplete homeothermy. The problem for bats, Young (1957) suggests, is that their surface area to volume ratio is enormous and there is little insulation in the membraneous wings. Small mammals are more susceptible than large mammals to changes in the external temperature for this reason.

Imperfect thermoregulation was first discovered in primates by Bourlière & Petter-Rousseaux (1953) and Bourlière et al (1956) although Shaw (1879) had noticed that in June (mid-winter) a captive Cheirogaleus was 'cold to touch .... and only with vigorous rubbing' and artificial warming could it be induced to become active. Both Microcebus murinus and Cheirogaleus medius exhibit seasonal fluctuations in activity, weight, food consumption and metabolism (Bourliere & Petter-Rousseaux 1966). Fatty tissue stored around the tail of Cheirogaleus (and Microcebus) provides the additional energy requirements during the periods of torpidity.[1]

Below 18°c both Microcebus murinus sub-species exhibit reduced activity. Martin (1972a) remarks that as temperatures in forests inhabited by M.m.murinus rarely fall below this figure it is unlikely to account for changes in activity. In the forests of Analamazoatra, however, the mean minimum temperature is for no month greater than 16.9° and between June and September overall mean temperatures are less than 18°c[2]. As M.m.rufus living in this region are smaller than M.m.murinus in the west, the control of heat dissipation may be more critical and thermoregulation correspondingly difficult.

For Dwarf lemurs, Petter (1962) described periodic variation in winter dormancy from 2 or 3 days (Cheirogaleus major) to one month (C.medius), and also reported short term cycles in tail fattening according to fluctuations in ambient temperatures.

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[1] It is not certain whether this is true of Microcebus in the wild (Martin 1972 a)

[2] An interesting and relevant consideration is whether an imperfectly homiothermic mammal would adopt the strategy of attempting to minimise heat loss during the coldest period (i.e. night) by remaining inactive (diurnal activity) or to raise the body temperature by moving and feeding at these times (nocturnal activity).

At present, data on lemur activity patterns in the wild are only available for species in which homeothermic abilities remain to be measured and a relationship cannot be assumed to exist. Richard described "sunning" behaviour in Propithecus verreauxi as of possible indirect thermoregulatory significance in reducing heat loss, and noted that it occurred more during the cool dry season than at other times of the year (Richard 1973). This was also the period of minimal activity period duration. The use of nests or holes is widespread in all lemur families except the Indriidae, and social sleeping aggregations or huddling behaviour, which is also heat conserving is probably practised by all lemur species during their non-active periods. Diurnality, basking, limited periods of feeding and gregarious huddling behaviours are quoted by Bartholomew & Rainy (1971) to effect homeothermy in the rock hyrax (Heterohyrax brucei) with a minimum of energy expenditure. These activities may have similar consequences for some prosimian species.

The relationship between environmental temperature and lemur behaviour may be complex. Increasing daylength has been shown, under constant temperatures, to induce reproductive activity in Microcebus (Petter-Rousseaux 1970, Martin 1972c) , and the drop in light levels is certainly the signal for activity to commence in at least two nocturnal species (Pariente 1974). The level of light alone, however, does not regulate activity in either Propithecus verreauxi (Richard 1973) or Indri indri, and other factors, probably including temperature, are involved.

Definitive criteria for 'activity' are often lacking in primate groups which may gradually engage in specific behaviours over considerable periods of time. Reports of clear environmental influences on active day length are, therefore, infrequent. Although some primates occupy environments with great changes in temperature between seasons (e.g. *Macaca fuscata*, *Macaca sylvana*) and where snow lay for some of the year, seasonal variation in activity period may not be acute (Deag 1974). Some terrestrial primates e.g. *Papio hamadryas*, *Papio cynocephalus* and *Macaca sylvana* sleep on cliff ledges or in trees and ascent/descent times can be recorded. Although these may vary from day to day Kummer (1968) found a significant correlation between morning descent times and sunrise for *Papio hamadryas*. Stoltz & Saayman (1969) suggested a very close relationship between activity and light levels for *Papio ursinus*. *Macaca sylvana*, in the Moroccan Atlas, appeared to climb into sleeping trees just before sunset but descend in the mornings at variable times (Deag 1974). Both for *Cercocebus albigensis* (Chalmers 1968) and *Cebus albifrons* (Bernstein 1965) activity patterns related to the time of dawn and dusk which, as for most primates, varies little seasonally in the tropical regions they inhabit.

Indri are often active for less than 50% of the daylight hours. If behavioural thermoregulation is of physiological importance for lemurs with a plentiful supply of food and a limited repertoire of active behaviours, Indri may profit from maintaining a short, continuous, diurnal activity period. It is conceivable that sleep occurring at times of good visibility is accompanied by night vigilance as most large Malagasy carnivores are nocturnal (Albignac 1973). Sympatric lemurs, however, do not follow this pattern and frequent observations suggested that Indri slept equally during the night. Long periods of uninterrupted rest may be required for digestion to occur satisfactorily.

Finally Hall (1962) and Altmann & Altmann (1970) have suggested that baboons may have longer activity periods when food productivity of an area is low. This either works in reverse for Propithecus verreauxi, as they are least active when the deciduous forests then inhabit are largely leafless, or is not a contributory factor. No measurements of food abundance were collected during the present study but the gradually changing activity period was not obviously correlated with the production of all or specific Indri foods. A direct connection between low motor activity levels and a folivorous diet mediated by a tight energy budget, is suggested by Charles-Dominique and Hladik (1971) both for diurnal primates (Indri, Alouatta, Colobus, Presbytis etc.) and the nocturnal lemur, Lepilemur mustelinus leucopeus.

6. SUMMARY

1. Indri are active for only part of the day. Compared to diurnal primates they become active late and cease activity early. The whole of the activity period is spent feeding or moving to food sources - a pattern which is interrupted only by short rests.

2. The timing of the activity period of Indri varies seasonally with daylength. It is likely that factors other than daylength also influence activity period duration but these could not be determined with certainty. Rain did appear to correlate with a late activity start and an early activity cessation, and, therefore, activity period duration but these correlations were not always significant. The start of activity each morning was not apparently affected by any one individual in the group.

3. The two study groups rose each day at the same time but Group V took up sleeping positions significantly later than Group P for most of the study period. Although weather conditions during observations on each group differed, this did not account for the difference in activity period duration.

4. 'Quiet' periods, when the whole group become immobile for periods lasting up to 40 minutes, and suckling bouts by the infant in Group V were unlikely to have caused this Group to extend its activity later in the day. Lactation of the Group V adult female may have

required her to feed more each day and thus retain a longer period of activity. The difference between groups may however have been due to differences in food availability.

5. Although most calls occurred during the first half of the activity period their timing was too variable for a simple relationship between activity start and the time of call to be proposed.

6. Mammals, including some primates, regulate their body temperatures imperfectly. Differences in the length and timing of the activity period in prosimians may be related to the need to reduce heat loss. Other possible influences on activity patterns are discussed.

CHAPTER 4

Group Composition and Population Density

1. INTRODUCTION

In this chapter the evidence for regarding Indri groups as 'family units' (Petter 1962) - an adult pair and their offspring - is presented and examined. With two exceptions all Indri found during the period of study were located in groups whose compositions were consistent with this view: (1) one group of 2 males, and (2) the (possibly seasonal) occurrence of solitary animals which were probably males (Chapter 9). In the following section on population density the former are taken into consideration. Evidence is presented elsewhere (Chapters 7 and 9) that solitary animals move across other groups' ranging areas at certain times of the year.

The complexity of ecological systems in tropical rain forest environments - the large numbers of species of plants and animals and their different habits and life styles - has contributed to the popular belief that such habitats are producers of abundant supplies of food for the constituent animals. However, detailed studies on primate feeding behaviour (Chivers 1974, Clutton-Brock 1975, Clutton-Brock (in prep.)) show that at least some species are highly selective in their choice of foods which may, in addition, be widely dispersed. Furthermore the production of food in the rain forest may be slow, sporadic and unpredictable (Medway 1972, Abrahams pers. comm.). Relationships between the supporting properties of a primate habitat and the primate biomass can be studied only by detailed observations and measurements of of population density, food availability and food competition amongst sympatric species (Hladik and Hladik 1972). An attempt is made in Section 3 to account, in these terms, for the comparatively low biomass of Indri and other lemurs in the eastern rain forest of Madagascar. It is important to attempt this ecological synthesis before trying to understand the functional significance and social organisation of Indri groups. The few ecological data obtained during this study are presented in this section for further discussion in the final Chapter 11.

2. GROUP STRUCTURE AND COMPOSITION

2.1. Introduction.

Even the most habituated forest-living primates cannot be continuously observed. Records of their behaviour may become distorted by a differential visibility of specific individuals and particular activities (Aldrich-Blake 1970 and see Chapter 2). In some species, for example, animals may be easier to spot if they are moving. By counting fully visible and partially concealed mangebeys during each census, Chalmers (1968) reported a higher 'exposure ratio' for moving animals compared to those engaged in sedentary activities. This is often an important factor as attempts to census primate species generally involve counting groups unused to being observed, with fleeing the most common immediate reaction. This augments the 'countability' but simultaneously reduces the chances of individuals being recognised or sexed. Members of primate groups tend to flee together but, if concealment is the secondary response to being chased, may differ individually (or by age/sex class) in the initiation of hiding behaviour.

Dense vegetation also interferes with accurate counts of animals. At Gombe Stream Primate Research Centre in Tanzania a continuous process of fission and reformation of chimpanzee ranging parties is easily monitored by reliable daily sub-group counts in the denuded or savannah areas, but presents a variety of problems to the observer attempting a census in nearby dense forest (Tutin, pers. comm.).

The numbers of individuals counted in animal societies may also be dependent on the technique employed by the observer to find them. Ideally, all the animals inhabiting a measured area are counted, but unless groups are recognisably distinct it is, in practice, impossible to guard against double countings. Rodman (1973) was careful to equalise the time spent searching for primates in all parts of the Kutai study area in Borneo, but interpretation of the census results was limited by an inability to distinguish individual groups.

It is particularly in environments of restricted observer movement, poor atmospheric conditions and high vegetation density that counting animals possessing large ranging areas requires the description and, ideally, control of bias. The time involved in locating lemurs during this study made such a control impractical.

2.2. Problems encountered in censusing Indri.

2.2.1. Locating Indri groups.

Indri groups were found either by chance, as they fed near a forest path or, more usually, by stalking animals after they had advertised their approximate position by 'calling'. If chased by the observer unhabituated groups would invariably be immediately lost although it is very likely that they did not move far but hid motionless in a suitable tree. On several occasions *Indri* groups which had fled the observer were relocated hours later within 100 metres of their original position.

Two obvious sources of error, both deriving from the observer's method of locating animals, could have influenced representative sampling of censused groups. The observer tended to find *Indri* groups which (1) had called nearby, and (2) were situated near a path (which usually followed the top of a ridge in the forest). The modal group size (3), encountered in 60% of the groups, was found equally in those groups located by either method (1) or (2) above. It is probable, therefore, that these factors did not adversely affect a representative sampling.

At Fierenana it is considered very likely that all groups enclosed in or partially occupying the study area were seen. At Analamazoatra good counts were made of 6 groups in 1972 and 3(2 of them recensuses) in 1973. Of all the groups inhabiting adjacent areas only 2, known to exist from their vocalisations, remained unobserved.

At Vohidrazana all the groups living in those parts of the forest through which the study area access path ran, were censused over the 15 month period.

2.2.2. Sex identification.

In habituated groups the sex of each group member was physically determined by observation of genitalia during the morning social urination/defaecation sessions. The external reproductive organs of both male and female *Indri* are inconspicuous by their small size and in being covered by thick fur and it was only at these times that the sex of adults could be satisfactorily identified. The sexes of 5 adult males and 3 adult females were identified in this manner.

Over a period of time certain behavioural correlates of sex in adult *Indri* were determined. Adult males in unhabituated groups would react to a potential predator (observer) by approaching it or remaining between it and the rest of the group, taking a position low in the forest, and by usually being the first animal to make the loud repeated alarm 'hoots' (see Appendix 6). 'Scent-marking' behaviour in this context would be performed only by the adult male. In contrast, adult females would not normally scent-mark or hoot but, after a short period of silent immobility (its duration proportional to the observer's proximity) would flee (often seen carrying an infant or very closely followed by a juvenile) in a wide arc away from the adult male and the observer. Shortly after she had left, the adult male would follow her.

During census walks the behaviour of all animals seen in a group was noted. As the behaviours of the adults within groups were normally quite distinct, the sex of adults could be identified by extending correlates of behaviour and sex in known groups to adults in briefly-encountered, unhabituated groups. Some groups found early in the study could have their constituents retrospectively sexed as, according to recorded behaviour, they contained unambiguously behaving individuals. Uncertainties were, however, classified as "unknown".

Most groups found in this study contained infants or juveniles. As the relationships young Indri maintain with animals other than their mother are distant - according to observations on the 3 habituated study groups - identification of adult females is considered to be accurate. Identification of sex by the behaviour of adult males, however, assumes that their characteristic positions and activities could not be adopted by other individuals, were the male absent. Although the consistent pattern of much of the behaviour in adults known to be male is suggestive of strict sexual dimorphism in adult behaviour, differences between study groups in other aspects of adult male behaviour (see following Chapters) must be regarded cautiously.

2.2.3. Age determination.

Censusing was performed throughout the study period. For any group found to contain a juvenile aged 6-12 months, whose physique and association with the mother are quite characteristic, an assumption was made of its presence in that group as an infant during the previous birth season. Having monitored the development of young Indri from 1 to 26 months of age, it was clear that due to the strictly seasonal occurrence of births, unhabituated animals up to 15 or 16 months could be easily aged. In the momentary glance allowed the observer of unhabituated Indri, animals older than this were generally indistinct in body size although one individual in Group P was clearly intermediary between the juvenile and the adults.

Ideally census work on a seasonally reproducing animal species should be made at the same time of the year as the ability to find animals may be a function of their reproductive state. Even where this is impossible it is instructive to attempt a determination of group composition changes over the study period. It is assumed not only that an infant was present in June 1972 (when most of the first census was carried out) in a group later found to contain a juvenile, but that no other changes in group composition took place in the intervening period.

2.3. Results.

Table 4.1 shows the actual or assumed group compositions in the 3 study areas immediately following the 1972 birth season. In the 18 groups of known composition there were 55 animals (mean group size: 3.1; mode: 3.0). The 3 study groups, all of whose members were sexed, together contained 5 females and 7 males - each group containing an adult

Key to TABLES 4.1 and 4.2

Sex determination = 'c' certain= 'b' behavioural (see text).

I$^+$ = infant first seen as a youg juvenile and assumed to have been present as an infant in that group in June 1972.

Assumed age categories (see text) :

A	Adult aged 9 years or more
A*	Adult-sized, aged 6-9 years
J2	Old juvenile aged 3-6 years
J1	Juvenile aged 1-3 years
UK	Animals of unknown age and sex, probably including a high proportion of females, especially those without infant
I	Infant

Location	Group	A♀	A♂	A*	J2	J1	1	UK	Totals
PERINET	P	1c	1c	1(♂c)	1(♂c)	1(♀c)	-	-	5
	V	1c	1c	-	-	-	1(♂c)	-	3
	NB	1c	1b	-	-	-	1	1	4
	NE	-	-	-	-	-	-	2	2
	W	-	1b	-	-	-	-	>1	>2
	U	-	-	-	-	-	-	>3	>3
	U2	-	-	-	-	-	-	2(c)	2
	S	-	1b	-	-	-	-	1	2
TOTALS	8	3	5	1	1	1	1	>10	>23
FIERENANA	1	1c	1b	-	-	-	1	-	3
	2	1c	1b	-	-	-	1	-	3
	3	1c	1b	-	-	-	1	-	3
	4	1c	1b	-	-	-	1	-	3
	5	1c	-	-	-	-	1^+	1	3
	6	1c	1c	-	-	-	1^+	-	3
TOTALS	6	6	5	0	0	0	6	1	18
VOHIDRAZANA	1	-	1b	-	-	-	-	2	3
	2	1c	1b	-	-	-	1	-	3
	12	1c	1b	-	-	-	1	-	3
	3	1c	1b	-	-	-	1^+	-	3
	4	1c	1c	1(♀c)	1(♂c)	-	-	-	4
	5	1c	1b	-	-	-	1	-	3
TOTALS	6	5	6	1	1	0	4	2	19

TABLE 4.1. *Indri* group composition in June 1972.

Location	Group	A♀	A♂	A*	J2	J1	1	UK	Totals
PERINET	P	1c	1c	1(♂c)	1(♂c)	1(♀c)	-	-	5
	V	1c	1c	-	-	1(♂c)	-	-	3
	nb								
	ne								
	w								
	U	-	1c	-	-	1	-	>1	>3
	uii								
	s								
TOTALS	3	2	3	1	1	3	0	>1	>11
FIERENANA	i								
	ii								
	iii								
	4	-	-	-	-	-	-	>2	>2
	v								
	6	1c	-	-	-	1	-	1	3
TOTALS	2	1	0	0	0	1	0	>3	>5
VOHIDRAZANA	i								
	2	-	-	-	-	1	-	2	3
	12	1c	1b	-	-	1	-	-	3
	3	1c	1b	-	-	1	-	-	3
	4	1c	1c	1(♀c)	1(♂c)	-	1	-	5
	5	1c	-	-	-	1	-	1	3
TOTALS	5	4	3	1	1	4	1	3	17

Key: as for Table 4.1, and,
Lower case letters and Roman numerals designate groups not recensused.

TABLE 4.2. Indri group composition in June 1973.

male and adult female.

Table4.2 lists the June/July compositions in 1973 of all those groups found. The noise produced by continuous hard rain during the 2 weeks allocated severely hampered recensusing during these months by obscuring sounds made by the animals which normally helped to locate them. In addition, all activities, including loud calls were reduced in bad weather.

Some conclusions may be drawn from the incomplete data presented.

2.3.1. Changes in the population.

In the groups accurately recensused in 1973 (8 in number), the total number of animals increased from 27 to 28 due to the birth of an infant in May 1973. Of all the groups that were recensused and which had originally contained an infant (6 in number) each possessed the expected juvenile. The successful rearing of infant Indri over the first year contrasts with observations on Propithecus verreauxi between 1970 and 1971 when 9 out of 10 infants born to four study groups died (Richard 1973).

2.3.2. Group composition.

Apart from one 2-male group, 14 of the 20 contained an adult female, the other 5 possessing individual(s) of undetermined sex. 17 of the 20 groups included 1 adult male, the remaining 3 with individual(s) of undetermined sex.

In all cases where information is available, lemurs have shown marked seasonality in the timing of mating and birth (Petter 1962, Petter-Rousseaux 1964, 1968, Jolly 1966, Martin 1972a, Richard 1973, pers. obs.). All 12 Indri infants which had been born in 1972 were of equal size at comparable times of the year and the seasonal reproduction of this species is therefore probably typical of the Lemuroidea. The Group P adult female produced no infant in 1973 and the close relationship with the two year old juvenile suggested that females may not give birth more frequently than every 2 or 3 years[1]. Group 4 at Vohidrazana contained in 1972 2 adult-sized Indri, the younger of which (by size comparison with Group P's juvenile) was at least 3 years of age and probably older. Unless one supposes infant mortality (for which there is no evidence) this supports the hypothesis that a mature female would only give birth every second or third year. Furthermore Group V, an adult pair with an infant of 7 months, exhibited no sexual behaviour during the 1972/3 mating season.

The adult-sized individual in Group P may have been sexually immature, showing little interest in the female during the mating season when she was, at least sporadically, attractive to the adult male. Copulatory attempts, by the adult male, observed on 4 occasions in Group P,

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[1] This group had been photographed in October 1970. It then contained 4 animals including one young individual who had been born in 1968 or 1969. This made the one certain known inter-birth interval either 2 or 3 years.

were aggressively rejected. The adult-sized male sniffed the female's genitalia occasionally at this time, but the absence of genuine sexual motivation in this individual, the relationships between adult females and their young aged up to 26 months, and body size differences form the informational basis for the conclusion that Indri groups occur largely as discrete families.

If the adult-sized male in Group P was an old but not yet sexually mature offspring, he was between 6 and 9 years of age. If sexual maturity occurred at about this age for both sexes and Group P contained 3 offspring born at 2 or 3 year intervals, the adult pair must have been in 1973, 12-17 years old. These two animals showed no signs of old age as classically itemized by the disputable criteria of patchy fur, baldness, 'sunken faces' (Jolly 1966). It is likely that this lemur is long-lived.

2.3.3. Reproduction.

By the end of the study 13 infants had been seen. 12 of the 20 groups had infants in 1972 and 1 group an animal aged 1 year. 11 of the infants were found in groups containing an adult pair only, one in a group of 3 and one in a group of 4 adult-sized animals. In addition, all 6 groups at Fierenana, the primary forest study site, consisted of 1 adult female with young and, in 5 of the 6 cases, 1 adult male. The sixth group contained an adult-sized individual of undetermined sex. All the infants at Fierenana had been born in 1972.

2.4. Discussion.

The study of changes in relative spatial displacement around their habitat remains of crucial importance in understanding the group compositions and social behaviour of primate species. Rigorous proof of strict monogamy would crucially affect the interpretation of the dynamics and behaviour of family-living primates, but to date, only in the Hylobatidae is there knowledge of specific pair-bond retention over several breeding seasons (Chivers 1974). The sexual fidelity of a single adult pair of animals must always be partially in doubt unless both can be continuously observed during the mating season. Retrospective identification of both adults in Group P was made from photographs of this group supplied by Dr. P. Charles-Dominique and Dr. A. Walker and taken in October 1970. Assuming that there was no seasonal sexual promiscuity it was probable that these 2 adults had continuously lived together in the same home range for at least 3 years.

If Indri do live in monogamous, exclusive families, a stable population may be thought to contain at least approximately equal numbers of groups of different size. These sizes range from 2 to a maximum depending on the maturation period and/or tolerance of sub-adults by other group members. Indri groups, it can be reasonably argued from the results presented above, normally contain a single adult pair with reproductive status and, in addition, other individuals who are infants or, in at least some cases, are clearly young - presumably offspring from previous breeding seasons.

It is, however, unlikely that any simple model for the generative development of a group of Indri from the first pairing of newly mature adults to the emigration of perhaps successive offspring, would easily account for the overall high frequency of infant-containing groups of 3, and the apparent synchrony in births between years. 12 of the 13 infants were born in 1972; 11 were born to adult pairs (all in 1972), 1 to a group of 3 animals (1972) and 1 to a group of 4 (1973). Even isolating the results from Fierenana, where all 6 groups located were of the minimum family size, leaves relatively large numbers of these 2 adult + infant groupings.

Synchronisation of births between groups can perhaps be more easily understood ecologically than sociologically. Sampling effected in a nutritionally favourable year, in peripheral regions of a population to which newly formed groups are displaced, might simulate the present results. Specific predation on juveniles (for which there was no evidence) might also contribute to explain apparent abnormality. At Fierenana a forestry survey performed in 1970 may have sufficiently disturbed Indri to leave the region only to subsequently recolonise it with newly formed adult pairs which all produced infants in May 1972. However, it might equally be that the results were indeed fully representative (or suffering only from random deficiencies of a small sample) and contain elements of information that define the organisation of a population as well as that of individual groups.

From the results presented in this chapter it is likely that Indri groups contain only one adult female and one adult male in reproductive condition and therefore differ from the larger groups of Propithecus verreauxi which frequently produce 2 infants (from 2 females) in a single season (Jolly 1966, Richard 1973). The indriids sympatric with Indri are Propithecus diadema diadema and Avahi laniger laniger, the former personally encountered in groups containing 2,3,1,2,3 and 5 (including an infant) individuals. Albignac (pers.comm.) reports sighting a group of 6 P.d.diadema including 2 infants and there may, therefore, be no difference in the 2 Propithecus species' normal group sizes. Unlike Indri the potentially close genetic relationships between Propithecus verreauxi group members is apparently diluted by males' mating season mobility (Richard 1974 a). Avahi laniger were encountered in 'groups' of 1,1,2,2,2,2*,3*, and 4 in these same forests, but it is easy to underestimate group counts of nocturnal lemurs.

In the size continuum of primate societies the formation of groups possessing more than one adult female in reproductive condition may require a fundamentally different system for the maintenance of social cohesion than in true families. Unless an ancestral condition has been especially retained, which seems unlikely (Charles-Dominique and Martin 1970), the discrete family unit has

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*including an infant

evolved in at least 3 major departments of the primate order: Ceboidea (Mason 1966), Hominoidea (Carpenter 1940, Ellefson 1968) and Lemuroidea. It is likely that an extensive behavioural comparison of groups of *Callicebus moloch*, *Hylobates sp.* and *Indri indri* will accelerate an understanding of the functional significance of family social systems (Crook 1970 and Chapter 11).

3. POPULATION DENSITY

A loud, continuously modulating call or 'song' (see below) is frequently heard in forests inhabited by *Indri indri*. Petter & Peyrieras (1974) estimated population density from measures of calling frequency, necessarily assuming two attributes of *Indri* behaviour: that all groups called over the study period, and that neighbouring groups were vocally different and could be acoustically distinguished.

During the present observations it was discovered that the tendency to call was a function of season, weather, proximity of adjacent groups and other undetermined conditions. Calling frequency was highly variable; in extreme cases several days silence would be interrupted by 4 or 5 vocalising sessions within a few hours (see Chapter 9).

It is reasonable to assume that over a lengthy study period all groups will call many times as most inter- and much intra-group communication is effected by this means but conclusions about population density made solely from vocalisation data exclude the essential discrimination between many calling groups and groups that call many times, and ignore the presence of consistently quiet individuals.

In the present study, estimates of Indri population density were made by two methods; one involved the counting of groups in an estimated area, the other the counting of groups in a known area (Table 4.3):-

(1) At Fierenana and Vohidrazana the groups found and/or regularly heard calling over the whole study period within an estimated radius of 1000 metres were either counted, or had maximum and minimum limits placed on the number of constituent animals according to the conclusions presented in the preceding section. This enabled maximum density limits to be assigned to each area as the audibly enscribed circle included only parts of the home ranges of some groups.

(2) At Analamazoatra the forestial region was more accurately measured by maps and aerial photographs. As most of the groups occupying this area were found and censused the densities lie within the stated limits. A bracketed adjustment is included which corrects for the presence of Eucalyptus plantations avoided by the animals.

The results from Vohidrazana should not be directly compared with Fierenana as the study position in the former site was specifically chosen so as to be able to hear the calls of many groups. However, the access path passed through the home ranges of 6 groups in 1500 metres, which is suggestive of a relatively high density.

TABLE 4.3. Population density estimates of *Indri*.

Location	1	2	3	4	5	6	7	8	9
FIERENANA	9	314^e	6	18	24	33	8-10	9	9
PERINET	9	282 (264)	6	18	24	33	8-11 (9-12)	10 (11)	11 (12)
VOHIDRAZANA	12-15	314^e	6	20	32	65	11-21	12-15	13-16

Key
1 Number of groups
2 Area in hectares. 'e' indicates estimated area of 100πha.
3 Number of groups with known complements
4 Number of animals in groups with known complements
5 Minimum number of animals in all groups based on the assumption that all groups with unknown complements contained 2 animals
6 Maximum number of animals possible in all groups based on the assumption that all groups with unknown complements contained 5 animals
7 Limits of population density (Number of animals/km^2)
8 Population density calculated on mean group size of the local population
9 Population density calculated on mean group size of all *Indri* groups.

Overall mean population density for all 3 study areas:
9-15 animals/km^2

Mean population density based on overall mean group sizes in all 3 study areas: 10-11 animals/km^2

The similar limits of the population density estimates in the three study areas (Table 4.3) must be considered as rough guides in highly selected areas. At Betampona near Tamatave, a warm coastal Forestry reserve, 5 *Indri* calls were heard over 3 days in early August 1972. All the calls were well over 1000 metres away from the observer, indicating far lower numbers than those in the three study areas which were, partially chosen for their high animal densities.

The estimate of 8-16 animals/km^2, corresponding to 3-5 *Indri* groups, is greatly in excess of Petter & Peyrieras (1974) calculations of 1 group/km^2 in one of the present study areas (Fierenana). The population density of *Indri* in this region is either changing rapidly or the anomaly results from the different methods of analysis adopted by Petter and myself. It was also suggested by Petter & Peyrieras (1974) that the population density in degraded areas increased as disturbed animals fled to quiet parts of the forest where large animal concentrations, and large groups, accumulated. In the present study comparison of the population structures - group size, composition and population density - in primary and partially degraded forests exposed no clear differences, though the sample size was small.

4. BIOMASS AND PRODUCTIVITY IN LEMUR HABITATS

4.1. Biomass.

By comparing the density of *Lepilemur mustelinus* in deciduous, gallery forest in the south of Madagascar with that of <u>Lepilemur</u> <u>mustelinus</u> plus <u>Avahi</u> <u>laniger</u> <u>laniger</u>[1] in the eastern rain forest of Analamazoatra, Charles-Dominique and Hladik (1971) have proposed that nocturnal folivores in the two different environments live at comparable concentrations. These authors claim that the biomass of this class of animal was probably superior in the east because the eastern subspecies of <u>Lepilemur</u> is larger. Further evidence for the similarity of the ecological 'supporting' properties of the two habitats came from comparisons of the respective population densitites of <u>Microcebus</u> <u>murinus</u> ssp.

This view is supported by Hladik and Hladik (1972) who report that the fruit and leaf-eating langurs, <u>Presbytis</u> <u>senex</u> and <u>Presbytis</u> <u>entellus</u>, of Polonnaruwa in Ceylon, live at a biomass (20-25 kgs/ha) comparable to folivorous primates both of the southern riverine forests e.g. Berenty and Antserananomby and the eastern rain forest e.g. Analamazoatra, in Madagascar.

To compare the relative body weights and population densities of leaf-eating lemurs from various parts of Madagascar (Table4.4), data from diverse sources were compiled. Only at Antserananomby was all information in one locality derived from the same observer at one time. Maximum figures for population density and animal weight are utilised.

The results support the Hladiks' (1972) argument that

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[1] It is very difficult to distinguish these 2 species at night in the forest.

TABLE 4.4 Comparable biomass estimates for leaf-eating lemurs in three regions in Madagascar

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(continued overleaf)

TABLE 4.4 continued

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Berenty and Polonnaruwa contained a similar total folivore biomass. However, the figures for Analamazoatra where Indri lived suggest a very low animal density despite the large numbers of leaf-eating species present. Riverine vegetation at Antserananomby supported a very high concentration of lemurs exceeding by 3-4 times the biomass estimate of the comparable Berenty environment. A proportionately similar difference separated the low biomass at Analamazoatra from that of Berenty. At Analamazoatra lemurs lived, compared to nearby forests, at a high density. All study areas in the rain forest contained either no Lemur rubriventer or Varecia variegata or very low numbers of these species.

There is consequently no reason to suggest that the biomass of folivorous malagasy primates in single-dominant gallery forests of the west and south are comparable with those of the eastern rain forests.

4.2. Dietary Overlap.

Irrespective of their biomass estimates, ecological competition between sympatric folivorous primates may be absent unless dietary overlap is proved. The evidence, summarised below, points to a high degree of dietary overlap between most sympatric folivorous species in Madagascar.

(a) ANTSERANANOMBY

Sussman (1972,1974) observed L.catta eating 21 species and L.f.rufus eating 11 species of plant. Nine of the 11 L.f.rufus food species were also L.catta foods. Although L.catta ate more flowers and herbs than L.f.rufus the 4 major species common to the diet of both lemurs accounted for 85.4% of the feeding records for L.f.rufus and 44.3% for L.catta. A single species, Tamarindus indica, eaten for 75.5% of all feeding records by L.f.rufus accounted for 24.4% of the feeding records of L.catta.

Although no comparable data was collected this dominant species was also a major food (an estimated 34% of the diet) for Propithecus verreauxi verreauxi at Berenty (Jolly 1966).

A preference for different levels of the forest may diminish to some extent direct ecological competition between species (Sussman 1974).

(b) BERENTY

Jolly (1966) found that 70% of P.v.verreauxi food species were also eaten by L.catta. The proportion of time that P.v.verreauxi spent feeding on species common to both the diets was 95%.

(c) ANALAMAZOATRA

Comparable data were not collected but the frequency with which observations of other lemurs' food species involved familiar species of plants, was impressive. The 8 observations in which a clear sight of the species of food eaten by Lemur fulvus fulvus was achieved, contained 6 of the major foods of Indri.

4 species were seen being eaten by Propithecus diadema diadema and at least two of these were important Indri foods.

4.3. Productivity of Primate Habitats in Madagascar.

(a) Eastern Rain Forests.

Unpublished reports describing limited but long-term observations on the phenology of rain forest trees were made available by the Centre Technique Forestier Tropical (CTFT). Studies were made in two regions:

(i) High, montane rain forest at Analamazoatra. The period of study lasted 7 years 4 months during which 17 common species (11 of which were major items in the diet of *Indri*) represented in 42 individual trees were regularly visited. 2 species (6 individuals) were deciduous.

(ii) Littoral rain forest at Foulpointe. The period of study lasted 4 years during which 21 common species (37 trees) were regularly visited. 3 species (6 trees) were deciduous.

Both these regions have high annual rainfalls. The wet season (December-March inclusive) accounts for 61.3% of the 2026 mm of rain at Analamazoatra and 48.3% of the 2778 mm rain at Foulpointe. The overall mean temperature at Analamazoatra is 19.0°c and varies from 15.5°c to 22.0°c through the year. At Foulpointe the overall mean temperature is 23.7°c and this varies from 20.2°c to 26.5°c through the year. Rain throughout the year keeps the mean maximum temperatures down to 27°c (Analamazoatra) and 31°c (Foulpointe).

The incidence[1] of flowers and fruits over the period

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[1] "Incidence" is the proportion of observations, expressed as a percentage, of any specific event, e.g. flower, fruit, compared to the total number of tree/years. Five trees observed for 4 years, for example, comprises 20 tree/years.

of observations, and the seasonal distribution of phenological events are summarised in Tables 4.5 and 4.6. At Analamazoatra 3 of the 42 trees did not flower once during the 7 years and 7 did not fruit.

Some new leaf production occurred annually in most species. This reconstituted the slight (<20%) defoliation which occurred just before or during the wet season. Flowers were observed throughout the year but least often during the wet season.

The relatively high figures at Foulpointe for the incidence of flowers and fruits may be misleading. The observations at Analamazoatra showed that a large variation could occur in these measures even between periods of as long as 4 years duration. Flowers and fruit incidence percentages during the first 3.3 years were 36.0% and 15.4% respectively, but over the following 4 years these figures dropped to 20.7% and 8.9%.

(b) Western Deciduous Forests.

The high seasonality of both climate and vegetation has been described by many observers (Petter 1962, Humbert & Cours Darne 1965, Jolly 1966). Both the study by Richard (1973) at Ampijoroa and the survey performed by the CTFT at Betsipotika and Marofandilia (Figure 4.1) support this conclusion.

At Ampijoroa rain falls only between October and April and is mostly confined to December, January, February and March (total annual rainfall 1608 mm). At Betsipotika and Marofandilia, which have similar vegetation and are both situated near Morandava, an identical

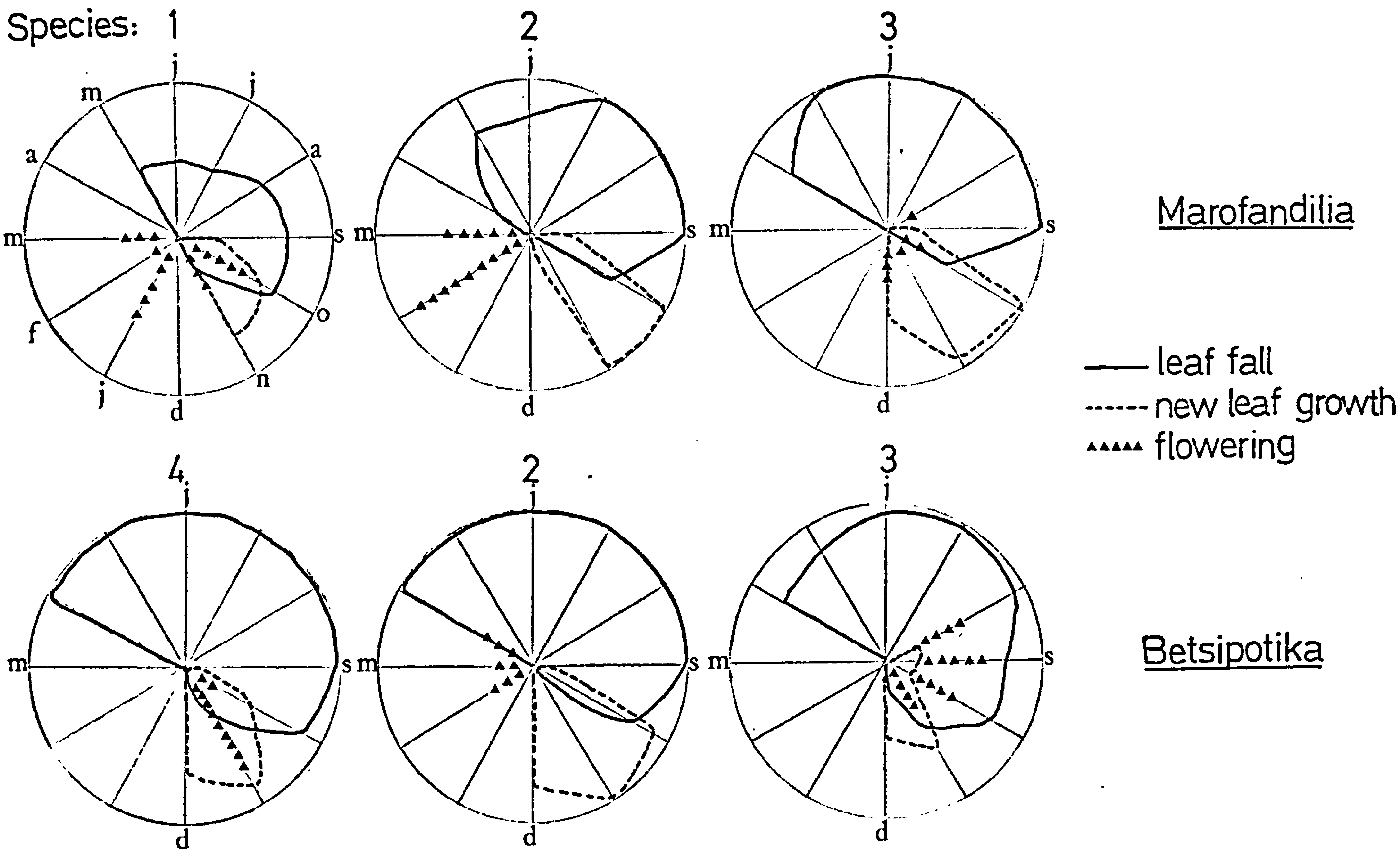
ANALAMAZOATRA	A	M	J	J	A	S	O	N	D	J	F	M
LESS leaves seen than the previous month	-	-	-	1	3	7	11	11	7	4	2	1
MORE leaves seen than the previous month	4	3	-	-	1	-	-	5	10	15	12	8
FOULPOINTE												
Presence of NEW LEAVES	58	49	56	56	29	19	23	23	15	36	49	55
Presence of FLOWERS	6	9	1	2	10	2	8	10	13	7	2	4

TABLE 4.5 Seasonality of leaf, flower production in the East.

EAST	INCIDENCE of FLOWERING	INCIDENCE of FRUITING	% FLOWERS to FRUIT
Analamazoatra (7.3 yrs)	25.3%	14.6%	57%
Foulpointe (4.0 yrs)	51.3%	37.8%	73%
WEST			
Ampijoroa (7 months)	6.2% (tree/months)	16.0% (tree/months)	-
Betsipotika (4.0 yrs)	63.4%	-	-
Marofandilia (4.0 yrs)	62.5%	-	-

TABLE 4.6 Incidence of flowering and fruiting in west and east (all % are tree/years unless otherwise stated).

Figure 4.1 Leaf fall, leaf flush and flowering in some common species of tree at Betsipotika and Marofandilia in the West of Madagascar.


Species: 1
2
3
4
2
3
j
j
m
a
a
m
s
o
f
j
n
d
Marofandilia
Betsipotika
leaf fall
new leaf growth
flowering

pattern is present but it rains overall much less (total annual rainfall 734 mm). The overall mean temperature at Ampijoroa is 26.7°c, varying from 24.4°c to 28.3°c. At Betsipotika the temperatures are similar but mean minima are up to 5°c below those of Ampijoroa.

A relatively high incidence of flowers was observed in these environments (Table 4.6). In all 28 trees (4 species) observed during the 4 years' observations at Betsipotika and Marofandilia, annual defoliation was followed by a complete reconstitution. At Ampijoroa (observation period 7 months, June - December) only 9 trees out of the sample of 100 trees (10 species) did not produce new leaves following the winter leaf fall.

The timing of the phenological cycles was found to be consistent across species (Figure 4.1). Leaf reconstitution typically occurs only during October and November at Betsipotika and Marofandilia. A burst of new leaf production was also observed in all 10 studied species at Ampijoroa during these same months, the beginning of the rainy season.

In Richard's study area (Ampijoroa) trees flowered at the same time or just after they flushed into new leaf. This was also observed at Betsipotika and Marofandilia (Figure 4.1).

4.4. Discussion.

Two main properties of the western forests serve to clearly differentiate them from those of the east:

(a) The higher turnover of potential foods in the west, in particular young foliage.

(b) The regularity of the changes in food productivity in the west. This occurs annually and coincides with the beginning of the wet season.

The main source of protein for lemurs in the west (young foliage) fluctuates seasonally in its availability. In the east, however, new leaf production is very limited as most trees are evergreen, but some seasonality is evident in leaf fall and reconstitution (Table 4.5). Individual trees of a species in the rain forests of the east, despite the high general density of the vegetation, may be widely separated (Black et al 1950, Janzen 1970). A high dietary specificity may thus require lemurs to live at low population densities.

Propithecus verreauxi observed by Richard (1973) had a high rate of infant mortality (9 of the 10 infants died) in the two main study areas. Richard also inferred a high rate of infant mortality (40%) for the same species at Berenty between 1970 and 1971. Between 1963 and 1964 Jolly (1966) claims that 2 out of 7 infants of this species died at Berenty. The Lemur catta population at Berenty reduced by 1 (153 - 152) between May 1972 and May 1973 despite the birth of 28 infants (Budnitz and Dainis 1975).

In the east all the 12 Indri infants born in 1972 survived for at least one year. No observations of individuals missing or disappearing were recorded.

Some relationships between the populations of folivorous primates and the productivity of the environments they inhabit may be tentatively suggested. The number of species of plants and the number of species of lemur is high in the east and low in the west. The density of specific plants and animals is low in the east and high in the west. The rate of turnover of both foodstuffs and animals appears also to be low in the east and high in the west.

Larger numbers of animal species may profitably exploit a relatively constant but low concentration of diverse foods in a stable ecosystem by living at low densities and reproducing at a low rate (EAST). High concentrations of fewer animal species may, however, inhabit regions with single-dominant forests (such as Berenty or Antserananomby in the WEST), where food is abundant seasonally and the population of lemurs subject to more acute fluctuations in animal density (Jolly 1966).

5. SUMMARY

1. _Indri_ live in small units of 2-5 individuals. Each group contains only one adult male and adult female and other individuals which are probably their offspring. One group (Group P) had contained 2 adults for at least 3 years and was probably a monogamous family group. _Indri_ probably give birth once every 2 or 3 years. Births probably occur in May.

2. The population density of _Indri_ in the 3 study areas lay between 8 and 16 animals (or 3-5 groups) per kilometre squared.

3. The total density and biomass of fruit and leaf-eating primates in the eastern rain forest appears to be low compared to the seasonal, deciduous forests of the west and south. There seems to be a relationship between the number of species, the density of the species, and the reproduction rate of both plants and animals in deciduous and evergreen forests in Madagascar.

CHAPTER 5

Local Spacing

1. INTRODUCTION

The parameters most often examined in analyses of social organisation in primates are social interactions between individuals (e.g. Hall and DeVore, 1965) and the distance separating individuals (e.g. Deag, 1974). Overt social interactions between group members in the present study were seen to occur at a frequency of about 0.4 per individual per hour of observation (see Chapter 8) and there were difficulties, therefore, in obtaining sufficient data for examining differences between relationships.

Early in the study it was noticed that some animals consistently adopted particular positions in trees according to the presence nearby of other group members. The adult male in Group V, for example, was rarely observed to feed in the canopy of a tree whilst the female was resting low in the same tree. The social influence appeared to be related more to relative position than to the distance between individuals and positional information describing which parts of the trees each individual was situated in was therefore collected for each Indri at each point - sample (see Chapter 2). In this way overall differences of the positions individuals took in the trees could be compared and subsequently related to (1) individual animal's activity, and (2) social situations in which other group members were nearby. In this way not only could those aspects of social communication be exposed which were not mediated by dynamic behavioural actions (e.g. vocalisations, tactile communication), but information about the relative positions of group members in occupied trees, of potential use in determining whether certain group configurations are strategically advantageous in locating or exploiting food distributed in certain ways (Eisenberg et al 1972), could be obtained.

In the following chapter the positions taken by individuals in the trees are compared both within and between groups. As individuals' positions changed less frequently than their activities, compared samples are composed of behavioural records which were collected at intervals of at least 30 minutes. More stringent levels of sample independence were achieved in this way (see Chapter 2).

2. FOREST LEVELS AS A MODEL OF SPACE

Small differences in individuals' physical capabilities and social constraints within the group defined the relative positions of Indri group members. Some observers, notably Kummer (1968), have described cases where the lower body weight and smaller size of females enable them to obtain food from terminal twigs whilst supported from branches incapable of sustaining a fully grown adult male. Unlike most Catarrhine monkeys, Indri adults exhibit no sexual dimorphism in size and differences between their positions in trees probably reflect only personal choice or social influences.

During some non-feeding activities the structure of the required support influenced the choice of parts of the trees they were performed in. For example, during the summer months play/wrestling between 2 and sometimes 3 individuals was frequently observed. Animals generally hung, suspended from a horizontal bough by one arm, in the lowest levels of the canopy (Plate 5.1). They engaged in contorted struggles that often ended in an agonistic interaction of considerable intensity. This was, therefore, a structurally demanding activity and was necessarily confined to particular supports. It was never seen in the central or top parts of the canopy.

The system of feeding demonstrated by Indri: visual selection of food from some distance, subsequently approaching the food, 'parking' in a suitable feeding posture, and consuming all the food available from that position, made behavioural transitions infrequent (see Chapter 2). Positional changes in trees appeared to occur as a function of food density, tree size and stability and the presence or absence of other group members.

The distribution of food within trees was heterogeneous. Lower parts of the trees, despite bearing foliage, were essentially structural whilst the tops of canopies seemed to be richly endowed with young leaves and fruit. No attempt was made to estimate the productive attributes of various parts of the food trees due to the excessive variability between trees, and difficulties in observing certain parts. Both the quantity of consumed food and the rate of ingestion were impossible to measure as both the techniques of feeding and the size of fruit and leaves were so variable (Chapter 6). Size differences

PLATE 5.1 Two young *Indri* 'play-wrestling' in Group P (Analamazoatra) at the bottom of the canopy.

in the study animals would also have affected quantitative estimates of food consumption.

No relation can be proposed, therefore, betwen the time spent by individual Indri in specific parts of the trees and the advantage gained by the individual in those locations. Differences within trees in the distribution of food were probably so great that each individual would normally have selected a similar feeding position if no other constraints were acting. Hence the choice of positions taken by several animals in the same tree is regarded primarily as a social phenomenon. Consistent positioning of individuals in certain parts of the trees or differences in their positions according to the presence other group members, assumes significance irrespective of whether those positions can be shown to be otherwise different or exceptional.

Nearest neighbour data and records of inter-individual distances do not contain information about the potential change in an animal's behaviour. This is because each part of the environment is assumed to be essentially identical to every other part. For arboreal folivorous primates, however, being positioned underneath the canopy of a tree generally means that food is unavailable and feeding is therefore impossible. The distance separating two individuals achieves greater significance if the activity of one is somehow limited.

3. RESULTS: LOCAL SPACING BETWEEN CANOPY LEVELS

3.1. The Sample.

A total of 1841 and 1017 records of the position of animals in the trees were obtained for Groups P and V respectively. Circuit I is omitted from both groups' data as poor habituation may have influenced animals' positions and the powers of individual identification were weak at this time. 'Terminal canopy' positions are combined due to the low numbers in the data from Group V. Terms such as 'terminal canopy' and 'canopy bottom' are defined in Chapter 2 .

The sample excludes all records where the canopy position of an individual could not be unambiguously defined. These occasions usually resulted from partial destruction of the tree or situation in lianes, and comprised in total 2.8% of the records.

3.2. Results: Differences between groups.

Indri at Analamazoatra spend approximately two thirds of their stationary time within the canopy of trees (Table 5.1). The central parts of the canopy seemed to be used about as often as the lower regions. *Indri* were less frequently observed in the highest canopy positions, however, although animals at these levels may have been more difficult to see.

Group P were found between 2 and 4 times more often in 'terminal canopy' positions than Group V, a difference too great to warrant statistical confirmation. Group V

Key to Tables (see Figure 2.3)

NC	No Canopy Structure
UC	Under the Canopy
CB	Canopy Bottom
TCB	Terminal Canopy Bottom
C	Canopy Middle
TC	Terminal Canopy Middle
CT	Canopy Top
TCT	Terminal Canopy Top

GROUP \ CAT		NC	UC	CB	TCB	C	TC	CT	TCT	
V	n	13	364	269	18	234	9	105	5	n=1017
	%	1.3	35.1	26.4	1.8	23.0	0.9	10.4	0.5	
P	n	52	514	467	83	455	46	190	34	n=1841
	%	2.8	27.8	25.3	4.5	24.7	2.5	10.3	1.8	

TABLE 5.1. Overall distribution of groups' canopy positions over the whole year

	UC	CB	C	CT
$X^2_{(1df)}$	19.07***	0.40	1.04	0.00

*$p<0.05$
**$p<0.01$
***$p<0.001$

TABLE 5.1a. X^2 values representing inter-group canopy differences

	UC	CB	C	CT	ΣTC	n
Ad♀	29.6	24.9	26.4	10.5	8.5	341
Ad♂	34.3	28.7	23.8	6.4	6.5	330
03	28.8	31.8	21.2	11.9	6.6	321
02	28.9	26.3	21.1	9.4	14.3	308
01	24.5	26.4	28.5	12.5	11.0	365

TABLE 5.2. Individual percentage distributions of canopy positions in Group P

	Ad♂	03	02	01
Ad♀	6.7	5.8	7.1	3.6
Ad♂		8.0	13.2*	17.2**
03			11.6*	10.0*
02				7.4

TABLE 5.2a. $X^2_{(4df)}$ values illustrating comparisons of overall canopy positions between Group P individuals

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Subject	Object	UC	CB	C	CT	ΣTC
Ad♀	Ad♂	1.6	1.3	0.5	3.8	0.8
	03	0.1	3.8	2.5	0.3	0.9
	02	0.0	0.2	2.5	0.2	↑5.4*
	01	3.0	0.1	0.1	0.4	1.0
Ad♂	03	2.3	0.7	0.7	5.9*↑	0.0
	02	2.1	0.5	0.7	2.0	10.0**↑
	01	9.2**	↓0.8	1.3	6.6*↑	3.5
03	02	0.0	2.3	0.0	1.0 ↑	10.2**
	01	2.1	3.0	↑3.9*	0.0	3.7*
02	01	2.2	0.0	↑3.9*	1.2	2.0

↑"object" significantly MORE

↓"object" significantly LESS

TABLE 5.3. Individual category comparisons between each Group P dyad. $X^2_{(1df)}$ values are shown for tests between each dyad for each canopy position in Group P irrespective of activity

spent considerably more time outside the canopy than Group P ($X^2_{1df} = 19.07$, $p<0.001$). Use of the lower, middle and higher parts of the canopy were similar in the two groups.

3.3. Differences between individuals.

Group P

If individuals of Group P are compared for differences over all categories only the adult male and the oldest (male) offspring, O3, are found to be distinct (Table 5.2). Each of these individuals spent significantly different proportions of time in the 5 categories compared with each of the two youngest offspring, O2 and O1 (Table 5.2a). There were no other overall differences between individuals.

A category by category examination of these 4 spatial relationships isolates where these differences lie (Table 5.3). O2 is seen to spend significantly more time in 'terminal canopy' positions than all group members except O1, and this accounted for most of the overall differences found between this individual (O2) and both the adult male and O3 animals. The adult male spent significantly more time out of the canopy and less time at the top of the canopy, than O1. O3 spent less time than O1 in the 'middle canopy' level. O1, in addition, is seen to have spent significantly more time in the canopy than O2. Finally, the adult male spent more time than O3 in the canopy 'top' level.

By referring to Tables 5.2 and 5.3 some conclusions may be drawn:

(i) In comparing every individual against every other individual in each category 20 tests are required per individual. The adult female of Group P was involved in only 1 significant difference whereas every other individual differed between 3 and 5 times. The adult female compared to others appeared in general terms to be intermediate in her use of various parts of the trees.

(ii) The adult male's behaviour contrasted with that of the adult female. He used top and terminal regions less than others and was more frequently encountered below the canopy altogether. When he did enter the canopy, therefore, he exhibited an affinity for lower regions.

(iii) The two youngest offspring spent more time than others in the terminal or top parts of the trees.

If each individual's canopy positions are related to those of the rest of the group combined, major differences are highlighted at the expense of sensitivity to small variations. In the 25 tests made there were only 4 significant differences, and these support the conclusions presented above: O2 spent significantly more time at terminal positions ($X^2_{1df} = 11.1$, $p<0.001$); the adult male spent significantly less time at the canopy top ($X^2_{1df} = 6.3$, $0.01<p<0.05$) and more time below the canopy ($X^2_{1df} = 5.6$, $0.01<p<0.05$); and O1 spent significantly less time than others outside the canopy ($X^2_{1df} = 5.9$, $0.01<p<0.05$).

Group V

The infant of Group V is considered separately (see Chapter 10) as at all times during the study his activity and positioning were closely allied to those of the adult female.

Analysis of combined data from all Circuits showed marked differences between adults' canopy positions (Table 5.4). The adult male spent significantly more time out of the canopy than the adult female ($X^2_{1df}=15.3, p<0.001$). She, however, despite spending more time in the 'middle canopy' ($X^2_{1df}= 14.9, p<0.001$) and 'canopy top' ($X^2_{1df} = 19.0, p<0.001$), avoided 'terminal positions' to virtual exclusion ($X^2_{1df}= 7.9, 0.001<p<0.01$).

3.4. Differences between individuals of different groups.

The proportion of time spent by both adults in various parts of the canopy were compared to investigate the origin of differences between groups (Table 5.5). When the adults only of each group are compared, it is only at the 'terminal canopy' category that a difference between the groups persists ($X^2_{1df}= 15.5, p<0.001$), the affinity of the Group P offspring for higher levels in the forests accounting for the original variation.

When adults of the same sex are tried against each other there are two results:

(i) the adult female of Group P spent much more time than her Group V counterpart at 'terminal positions' ($X^2_{1df}= 20.6, p<0.001$), and rather less at the canopy 'top' ($X^2_{1df}= 3.9, 0.01<p<0.05$);

(ii) the adult male of Group P spent significantly more time than his Group V counterpart in the 'middle canopy' ($X^2_{1df}= 6.4, 0.01<p<0.05$), and less time below the

		UC	CB	C	CT	ΣTC
Ad♀	%	29.4	25.8	27.7	15.4	1.5
Ad♂	%	42.9	29.8	16.3	6.1	5.0
$X^2_{(1df)}$		15.3^{***}	1.5	14.9^{***}	19.0^{***}	7.9^{*}

TABLE 5.4. Individual differences in Group V canopy positions (% time spent in each category by each individual & $X^2_{(1df)}$ values between individuals).

Comparison	UC	CB	C	CT	ΣTC
V versus P	1.6	0.5	1.1	1.9	15.5^{***}

TABLE 5.5. X^2 values illustrating gross canopy position differences between combined adults of each group

Subject	Object	UC	CB	C	CT	ΣTC	$X^2_{(4df)}$
Ad♀	Ad♂	0.0	$^{**}7.7$↑	0.0	2.9	1.7	10.2^{*}
	03	0.1	$^{*}4.3$↑	2.6	0.5	0.3	5.9
	02	0.0	1.9	$^{*}5.8$↓	0.1	3.6	8.2
	01	1.1	2.1	2.4	0.0	1.3	5.3
Ad♂	03	0.0	0.5	2.3	$^{*}5.1$↑	0.5	6.6
	02	0.0	2.1	$^{*}5.1$↓	2.1	$^{*}8.5$↑	13.7^{*}
	01	0.6	2.3	2.1	3.6	$^{*}5.3$↑	11.1^{*}
03	02	0.1	0.5	0.5	0.9	$^{*}5.4$↑	5.9
	01	0.4	0.5	0.0	0.3	2.7	3.3
02	01	1.0	0.0	1.0	0.2	0.7	2.3

↑object MORE

↓object LESS

TABLE 5.6. Overall (4df) and category by category (1df) examination of individuals' canopy positions in Group P. The X^2 values of tests between feeding individuals are shown for each pair of animals at each canopy level

canopy ($X^2_{1df} = 5.6$, $0.01<p<0.05$).

When each adult was compared with the neighbouring group's adult of the opposite sex, it was the adult differences within Group V that were essentially retained:

(i) the adult female of Group V, for example, spent significantly more time than the adult male of Group P in the canopy top ($X^2_{1df} = 15.0$, $p<0.001$), but significantly less time in the terminal parts of the canopy ($X^2_{1df} = 13.4$, $p<0.001$);

(ii) the adult female of Group P spent significantly more time than the adult male of Group V at both 'middle canopy' ($X^2_{1df} = 11.0$, $p<0.001$) and canopy top ($X^2_{1df} = 4.8$, $0.01<p<0.05$), but less time below the canopy ($X^2_{1df} = 13.6$, $p<0.001$).

4. LOCAL SPACING WHEN ANIMALS WERE FEEDING

4.1. Differences between groups.

Inter-group differences in canopy use when animals were feeding followed closely those found irrespective of activity. Group V fed considerably more (17.4%) than Group P (9.9%) on foliage and fruit from trees other than those in which the animals were situated[1] ($X^2_{1df} = 12.52$, $p<0.001$). In 'terminal canopy' positions Group V fed for 100% of the time, whereas Group P fed there for 69.5% of the time. These differences serve to reduce the ecological significance of overall variation between groups' positions in the trees.

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[1] This type of feeding is henceforth called 'feeding on non-supporting vegetation'.

4.2. Differences between individuals.

Group P

Individual differences in 'feeding' canopy positions (Fig.5.1) were comprehensively tested (Table 5.6). Reference to overall canopy use irrespective of activity (Table 5.2) enables major activity differences ('Feeding' and 'Not Feeding') to be compared. Only 3 of the differences found overall are identical to those for feeding records only: O2 spent more time in terminal positions than the adult male and O3; and O3 both fed and rested more than the adult male in the 'middle canopy'.

New differences were also revealed. The adult female fed relatively less at 'canopy bottom' than either adult; and O1 was found to feed significantly more in terminal canopy positions than the adult male. As for those found irrespective of activity (Table 5.2), it is the adult male who figures prominantly in inter-individual feeding position differences.

In general, canopy level differences between the adult male and the two youngest offspring, O2 and O1, are independent of activity. In addition, the canopy levels taken by the adult female when feeding significantly differ from those taken by the feeding adult male.

Group V

The adult male not only spent more time than the adult female in the 'terminal canopy' but also fed there more. The adult female not only spent more time than the adult male in the canopy 'top' but also fed there more

Figure 5.1 The proportion of time each individual in each study group spent in various parts of the tree (see Fig. 2.3) when feeding.

GROUP P
GROUP V
% feeding records
40
20
0
40
20
0
♀
♂
3
2
1
♀
♂
under canopy
canopy bottom
canopy middle
canopy top
terminal canopy

(Table 5.7). The adult female spent significantly more time in the 'middle canopy' than the adult male but this difference was devoted to non-feeding activities. Similarly, although the adult male spent 43% of the time under the canopy levels compared to the female's 29%, the latter fed there rather <u>more</u> than the former.

Group V, therefore, exhibited activity-dependent positional differences between the adults.

(iii) Differences between individuals of different groups

Overall differences between adult females were found to lie in the proportions of time spent in canopy top (V more) and terminal canopy (P more) locations. When feeding, however, the Group V adult female preferred 'under canopy' positions ($X^2_{1df} = 6.5$, $0.01<p<0.05$) compared with the adult female of Group P, although altogether they spent similar proportions of time there. No difference existed between the two adult females in the proportion of time spent feeding at 'canopy top' but the Group P adult female fed more frequently at terminal positions than the adult female of Group V ($X^2_{1df} = 19.6$, $p<0.001$).

Activity-independent canopy level differences between adult males were distinguished by the Group V adult male's relative preference for remaining under the canopy and avoidance of 'canopy' positions. The proportion of time spent feeding at these levels were, however, similar.

		UC	CB	C	CT	ΣTC
OVERALL	♀	29.5	25.8	27.8	15.4	1.5
	♂	42.8	29.7	15.3	6.0	5.0
FEEDING	♀	19.5	19.5	33.6	24.0	3.2
	♂	13.6	24.8	36.0	9.6	14.0
NOT FEEDING	♀	41.0	32.9	20.7	5.3	0.0
	♂	57.0	32.0	6.6	4.3	0.0

TABLE 5.7. Group V adult differences in activity-dependent canopy utilisation (% time spent in each category for each activity)

	UC	CB	C	CT	ΣTC
OVERALL	15.3*** ↑	1.5	14.9*** ↓	19.0*** ↓	7.9** ↑
FEEDING	2.0	1.3	0.2	10.9*** ↓	18.2*** ↑

↑Ad ♂ HIGHER

↓Ad ♀ HIGHER

TABLE 5.7a. $X^2_{(1df)}$ values for tests between Group V adults' 'feeding' and 'overall' canopy utilisation

5. SUMMARY OF CANOPY LEVEL DIFFERENCES BETWEEN AND WITHIN GROUPS

Each individual's affinity for each of 5 canopy divisions was calculated for (a) all activities, and, (b) feeding activities only.

(i) In the large group (Group P) the adult male spent more time lower in the trees than most other group members, both for engaging in feeding and non-feeding activities. The adult female of this group was only different from others (being generally higher) when feeding. Amongst each other, the offspring of the group revealed canopy level differences overall but not for feeding activities only.

(ii) Compared to her adult male the adult female of Group V avoided terminal canopy positions. She only entered these parts of the tree in order to feed. The adult male spent more time not feeding under the canopy and less time not feeding at the 'middle canopy' level than the adult female. The adult male of this group also spent less time feeding than the adult female in the top of the canopies.

(iii) Overall differences between groups could be largely attributed to the presence of offspring in Group P. Only the inter-group difference in the terminal canopy scores (V low) remained when the younger animals were omitted from the test. This difference remained when feeding records only were tried and, by cross comparing each adult with each other adult, could be clearly shown to be due to evasion of the position by the Group V adult female. Similarly, the tendency for Group V to feed more than Group P under the canopy (i.e. feeding on non-supporting vegetation) was largely due to the fact that the Group V adult female fed much more there than the group's adult male. The Group V adult male remained lower than his counterpart in Group P whilst engaging in activities other than feeding, but these two animals fed equally at each level.

In both groups, therefore, in the context of greatest competition (feeding), the adult females stayed higher than the adult males in the trees. The adult females from the 2 groups exhibited more feeding level differences than did the two adult males.

6. SOCIAL INFLUENCES ON LOCAL SPACING

6.1. Introduction.

The individual activities of group-living mammals are not independently organised (see Chapter 2). Feeding behaviour in Indri is a social activity - different animals affecting to various degrees the synchrony of behaviour (see Chapter 6) and position between individuals.

To examine the possibility that those parts of the trees which individuals occupied differently were at least partly determined by social factors, the interdependency of animals' canopy positions was investigated.

Each record of two animals' simultaneous canopy positions was extracted from the sample. Pairs of animals were often seen together in large, dense food sources such as a tree in fruit and this selection from the data may have constituted a bias. It is assumed that the direction and magnitude of the bias did not differ greatly between pairs of individuals.

The effect of one animal on another's position in the tree could not be determined with certainty. This was because specific individuals had different tendencies to associate[1] together (some spatial relationships were stronger than others) and the whole group would move more or less together to feed in large trees. Difficulties consequently arise in isolating single pairs of animals when others could not have influenced the situation. For example, it was often impossible to be sure that no other individual was within a certain radius of the subject, and this made extraction of records when no <u>more</u> than 2 animals were visible, pointless. Furthermore, the abundance and variety of available supports in a tree could restrict the numbers and positioning of animals within it.

For these reasons it is profitable to first pursue information about the frequency of individuals' dispositions to feed in the same tree as others before discussing the social implications of relative, simultaneous canopy positions.

6.2. Results.

6.2.1. The frequency with which pairs of animals were in the same tree.

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[1] "Association on this and subsequent pages refers to the frequency with which two (or more) individuals were seen in the same scan at each point-sample.

Group P

Any two animals seen together, irrespective of the presence of others, associated in the same tree differently (X^2_{9df}= 21.07, 0.01<p<0.02). Only pairs including the adult female were notably distinct (Table 5.8). Of the 90 possible combinations of pairs of animals there were only 8 significant differences. Five of these significant differences emphasised the relatively low tendency for the two adults to be found in the same tree, and the remaining 3 significant differences focussed on a similar relationship between the adult female and the oldest male offspring.

O2 was the individual most often seen in the same tree as at least one other group member but the dyadic relationship in which two individuals were the most often seen in the same tree was formed by the adult female and juvenile.

Group V

The percentage of observations that both adults were situated in the same tree was significantly lower than all other pairs of animals in the neighbouring group (Table 5.8).

6.2.2. The frequency with which animals were seen simultaneously.

To some extent the difference between real and observed spacing may be examined by comparing the latter to the frequency that each member of a pair of animals were seen together i.e. at the same time, irrespective of the tree they were in.

No	Relationship	No. obs. SAME	No. obs. DIFF.	% SAME	Dyad Pair	X^2 (1df)
1	V Ad♀ + Ad♂	82	166	33.1	12	4.6^{*}
2	P Ad♀ + Ad♂	69	89	43.7	24	7.8^{**}
3	+ O3	77	83	48.1	25	12.5^{***}
4	+ O2	86	58	59.7	27	8.5^{**}
5	+ O1	133	81	62.1	29	7.1^{**}
					211	6.4^{**}
6	Ad ♂ + O3	62	52	54.4		
7	+ O2	82	53	60.7	34	4.1^{*}
8	+ O1	84	75	52.8	35	7.3^{**}
					37	4.7^{*}
9	O3 + O2	85	59	59.0		
10	+ O1	85	78	52.1		
11	O2 + O1	97	71	57.7		

TABLE 5.8. "SAME-TREE" association frequencies with significant X^2(1df) tests for all inter-dyadic combinations

Group P

Two relevant differences were encountered (Table 5.9):

(i) The adult female was seen approximately equally in association with all other individuals except the juvenile. Mother-juvenile association measures were significantly higher than all others.

(ii) Other individuals appeared to be more discriminating in their various associations. The adult male, for example, spent significantly less time than all others except 02, with the 03 individual. Conversely, 03 spent significantly less time near the adult male than any other group member.

Group V

The much closer spatial relationship between the adult animals in Group V compared to their Group P counterparts is clearly evident in the high percentage of time that they were seen together.

Comparing associations between pairs of animals in (a) the same tree, and, (b) overall, reveals some important features of the form of social influences on spacing within groups of Indri:-

(i) The adults of Group P spent significantly more time in the same tree and significantly less time associated overall, than the adults of Group V, and,

(ii) Differences between 'association' measured by (a) same-tree scores and (b) overall scores, were great. Of the 9 significant differences between pairs for overall association, only 2 were common to 'same-tree' association scores. The ability to predict the tendency for individuals

Object

Subject	Ad♀	Ad♂	03	02	01
			←	*** ←***	→ →
Ad♀		46.3	46.9	42.2	62.7
		←	***		→
			←	***	→
Ad♂	47.9		34.5	40.9	48.2
	←	***	→		
	←***	→	← *	→	
03	49.8	35.5		44.9	50.8
		←	***		→
		←	**		→
02	46.8	43.6	46.8		54.5
01	50.1	43.6	44.7	46.0	
Overall mean	43.3	36.2	37.3	38.0	46.1

	Ad♀	Ad♂
Ad♀		60.9
Ad♂	65.3	

GROUP V

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

TABLE 5.9. Percentage of subjects' IAR's that each other individual (object) was seen in association with it.* Significant differences between dyads (←*→)

		SAME TREE			SEPARATE TREE			
S Subject	O Object	S higher	O higher	n	S higher	O higher	n	
Ad♀	Ad♂	61.4	38.6	26	64.8	35.2	51	Group P
	03	51.0	49.0	41	44.7	55.3	47	
	02	55.0	45.0	40	63.9	36.1	36	
	01	53.1	46.9	47	37.3	62.7	51	
Ad♂	03	56.0	44.0	32	38.4	61.6	26	
	02	53.2	46.8	32	36.4	63.6	33	
	01	40.8	59.2	32	23.1	76.9	52	
03	02	50.0	50.0	44	48.6	51.4	33	
	01	41.2	58.6	34	54.2	45.8	48	
02	01	37.5	62.5	40	35.7	64.3	42	
Ad♀	Ad♂	85.7	14.3	56	69.6	30.4	112	Group V

TABLE 5.10. Differences in relative canopy level of simultaneously observed individuals of Group P

to be found in the same tree, therefore, did not arise from measures of the frequency that they were seen together despite their significant correlation ($r^S=0.63$, $n=10$; $0.01<p<0.05$).

From comparisons of different measures of spatial affinity there appeared to be 4 types of spatial relationship:[1]

(i) relationships where 2 animals stay close to each other whether they are in the same or different trees,

(ii) relationships where 2 animals are often in the same tree but infrequently observed in proximity overall,

(iii) relationships where 2 animals are infrequently observed either in the same tree or in different trees, and,

(iv) relationships in which 2 animals are frequently observed together overall, but are rarely encountered in the same tree.

Examples of (i) and (iv), above, are easy to identify in the relationship of the Group P adult female with her juvenile, and the relationship between the two adults of Group V, respectively. A distant relationship, both overall and in same-tree measures, (iii) above, is exemplified by the relationship between the adult individuals of Group P. It is in case (ii), above, where individuals remain generally far apart but, when they <u>are</u> seen together remain essentially close (e.g. the Group P adult female

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[1] It is not intended to imply that these 4 types of spatial relationship are discrete rather than graded into each other. They are mentioned here as of empirical significance in distinguishing relationships observed during the course of the study.

and the O2 individual), that the possibility of constructing a simple model for spatial relationships in Indri is seen to become more remote.

7. SOCIAL INFLUENCES ON INDIVIDUALS' CANOPY LEVEL UTILISATION

7.1. Introduction.

Differences between individuals' overall canopy positions (Table 5.2) have been already discussed. It is the object of this section to consider how the form of the distributions vary in different social contexts. The question posed, therefore, is "does the presence of a specific individual in one part of the tree affect the situation of other individuals?".

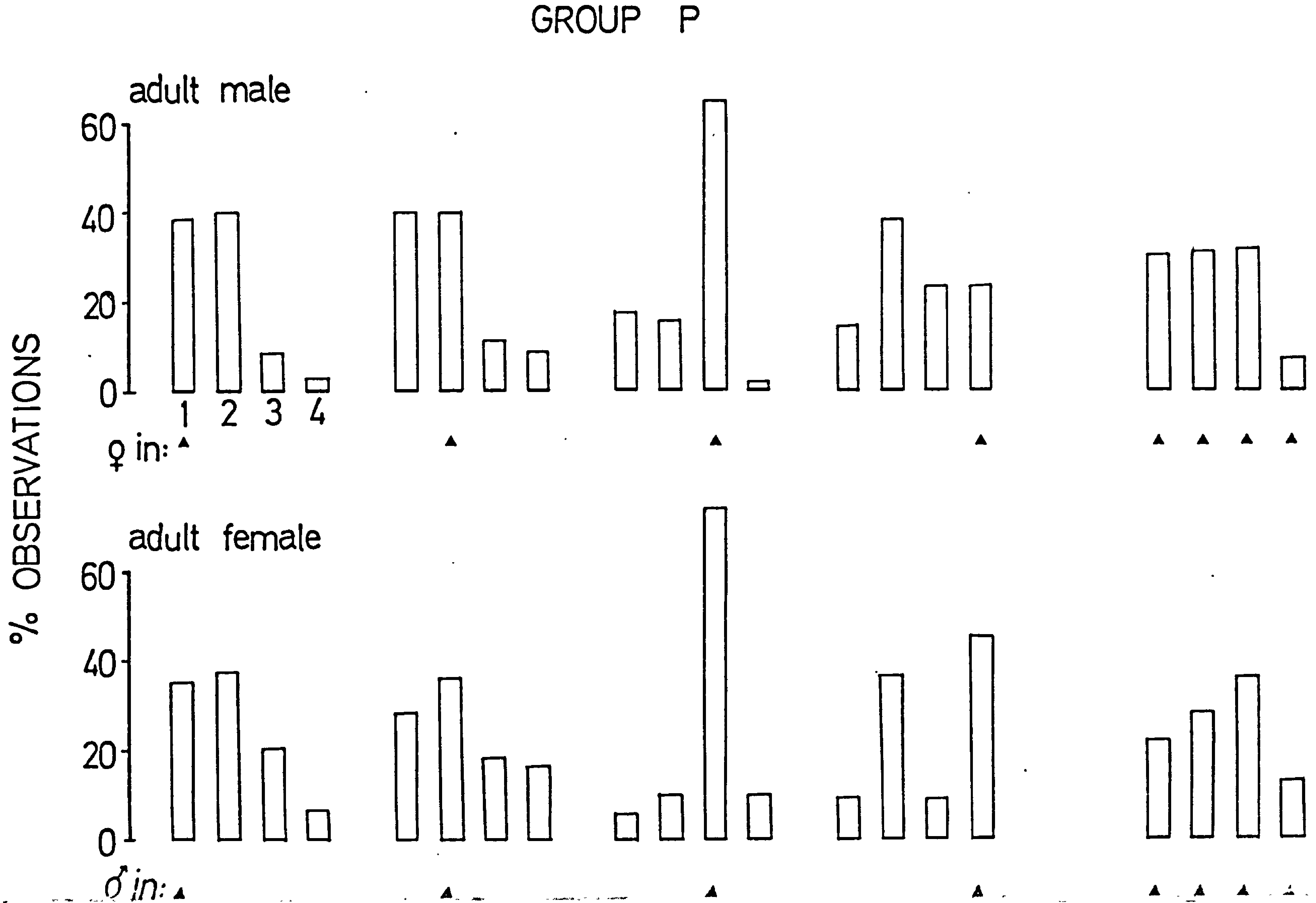
A high degree of behavioural synchrony is present between group members in the positions taken at the same time (Figure 5.2). As a general rule the highest percentage of time spent by each individual at a canopy level, occurs when another animal simultaneously seen is itself at that level. This relationship holds for all animal pairs with 3 exceptions. These exceptions are all in Group P and all involve the adult female:

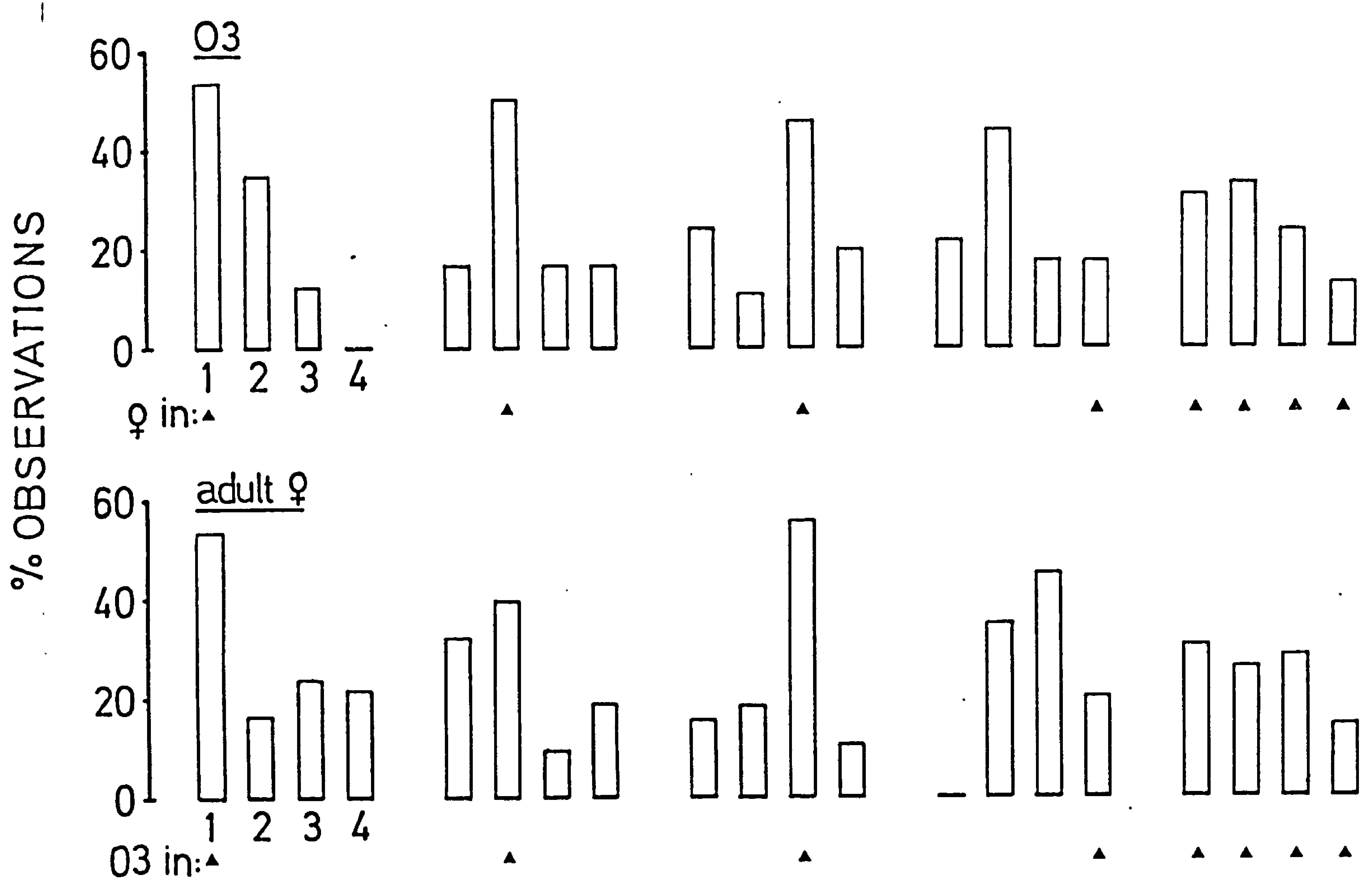
(i) The adult male spent more time below the canopy when the adult female was in the 'middle canopy', than when she was herself below the canopy.

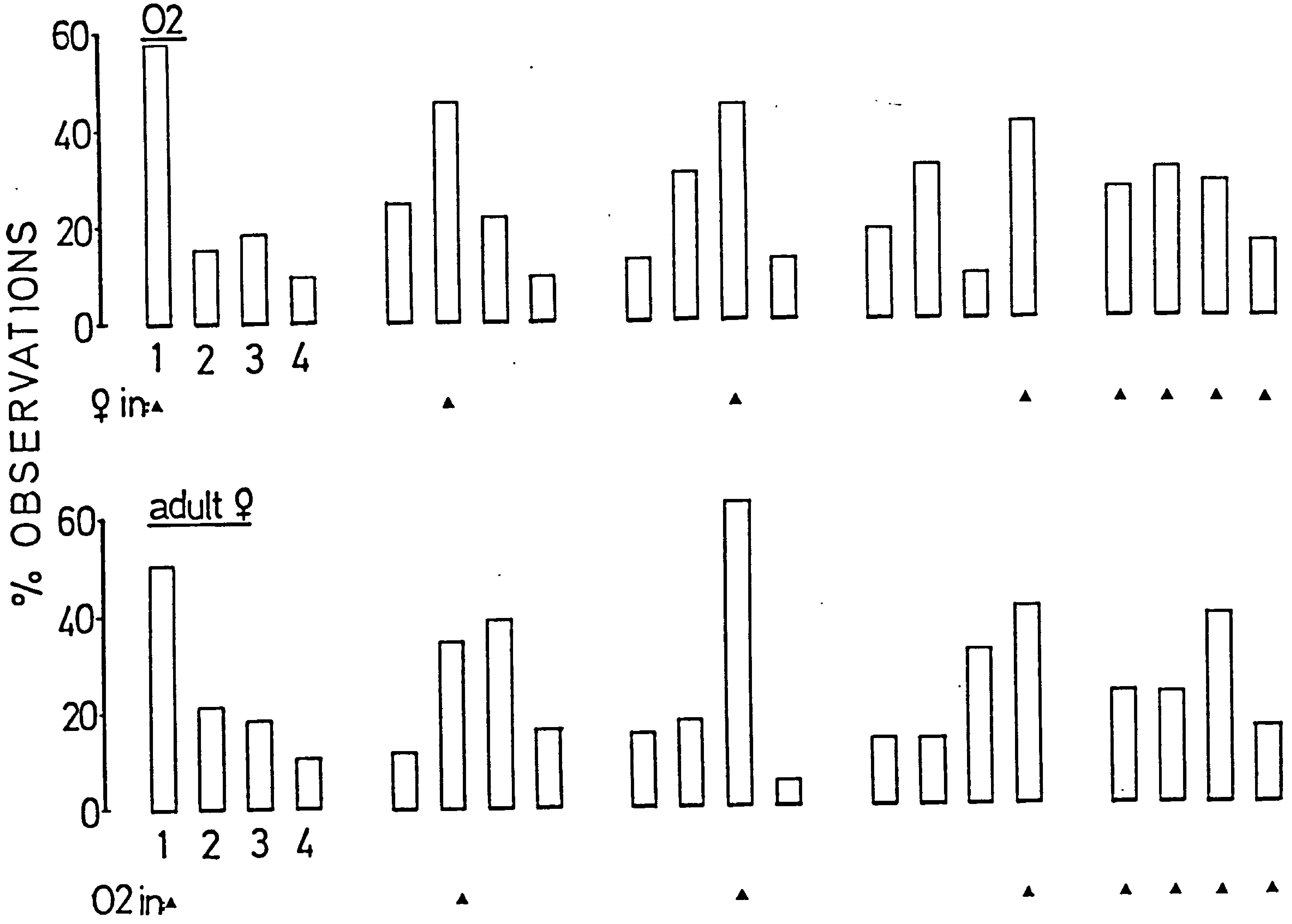
(ii) The adult male spent the same amount of time in the bottom of the canopy when the adult female was below the canopy as when she was herself at 'canopy bottom'.

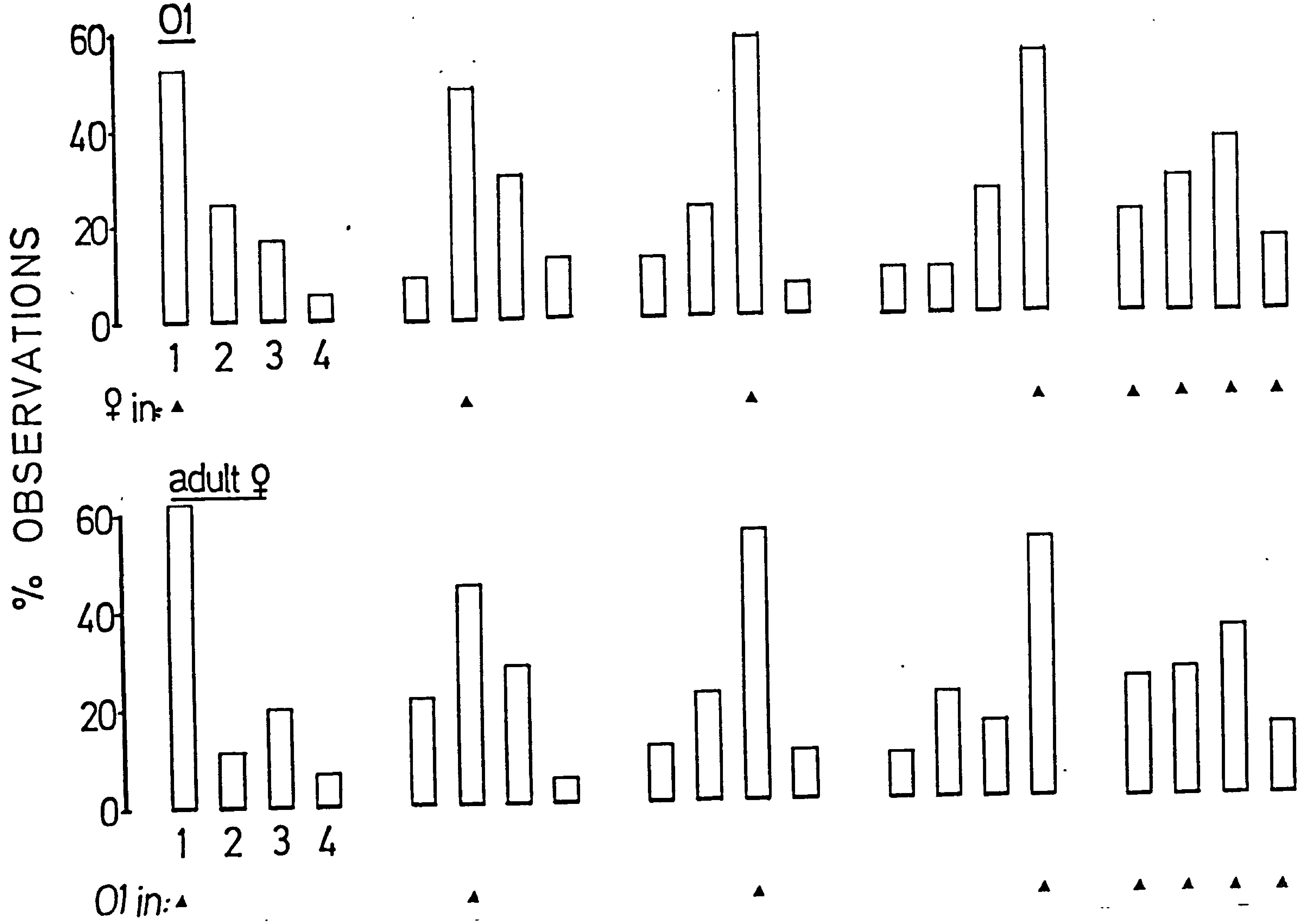
Figure 5.2 The proportion of time each individual spent in each part of the trees (see Fig. 2.3) when each other individual in the same group was simultaneously seen in every other part of the trees.

Each histogram represents the proportion of observations of the subject in categories 1 (under canopy) , 2 (canopy bottom) , 3 (canopy middle) and 4 (canopy top) according to where the subject's partner is situated. The final histogram in each set represents the proportion of observations of the subject in each category irrespective of the situation of the simultaneously seen partner.

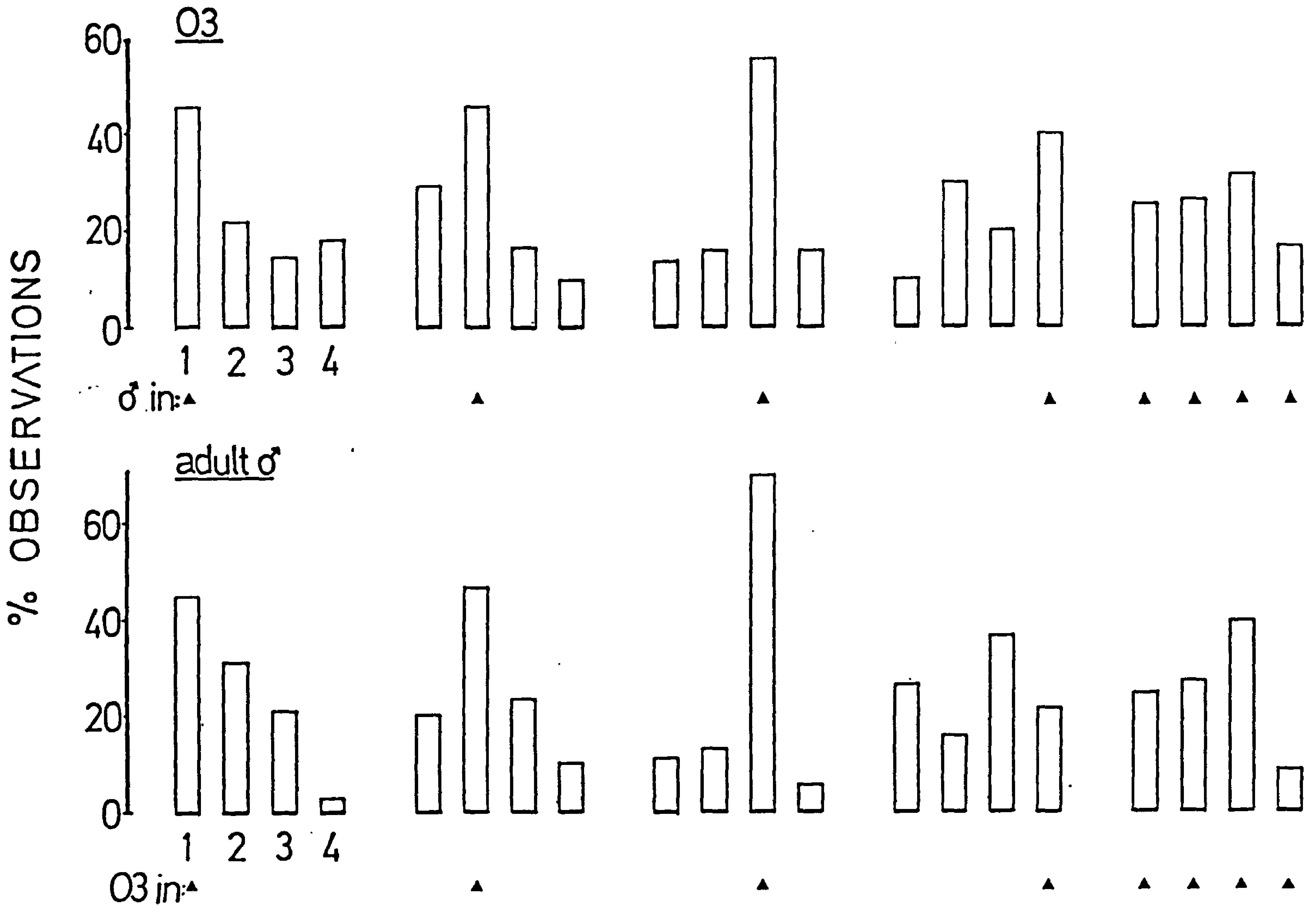

GROUP P
adult male
% OBSERVATIONS
60
40
20
0
1
2
3
4
♀ in:
adult female
60
40
20
0
♂ in:

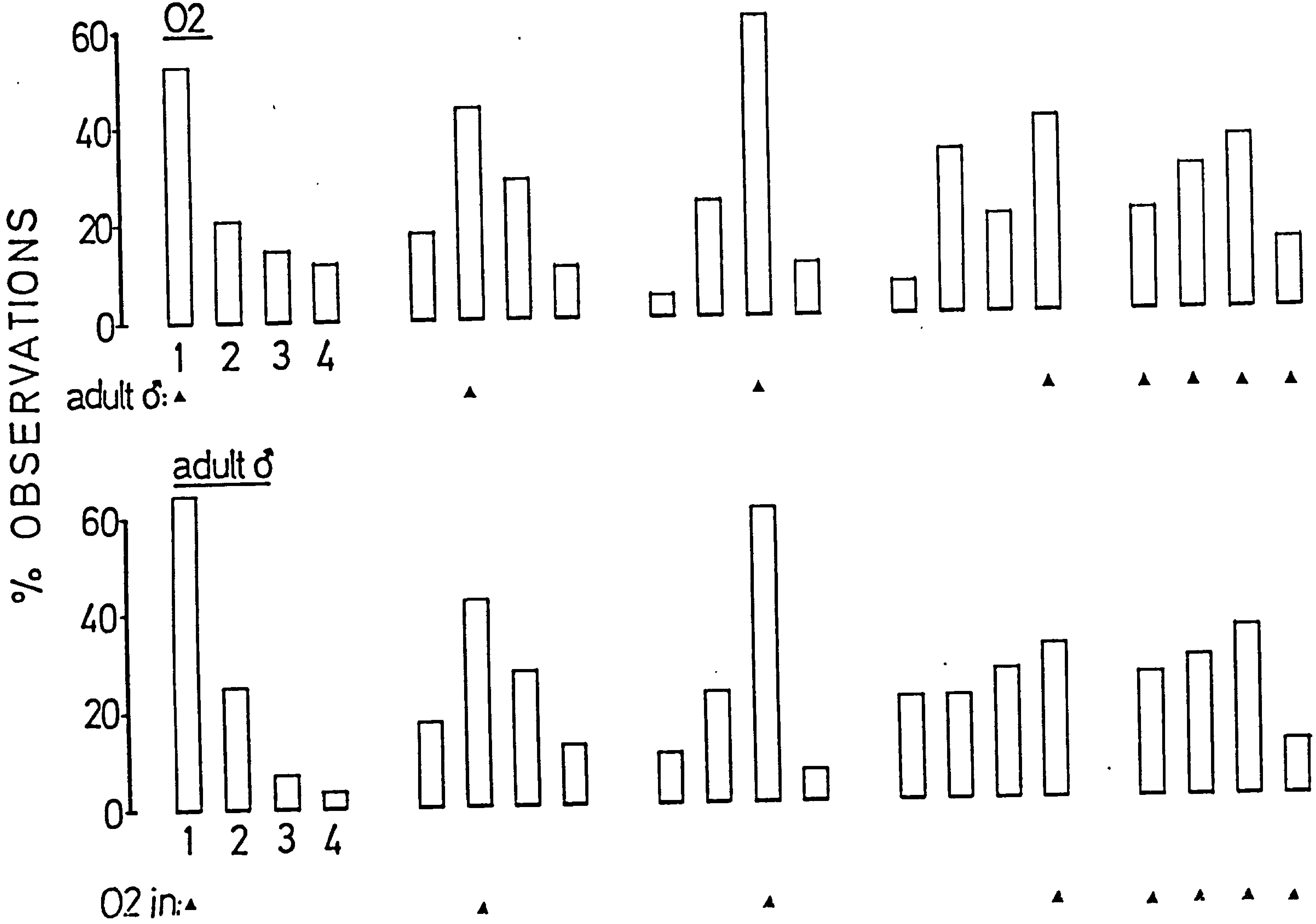

% OBSERVATIONS
O3
60
40
20
0
1
2
3
4
♀ in:▲
adult ♀
60
40
20
0
1
2
3
4
O3 in:▲

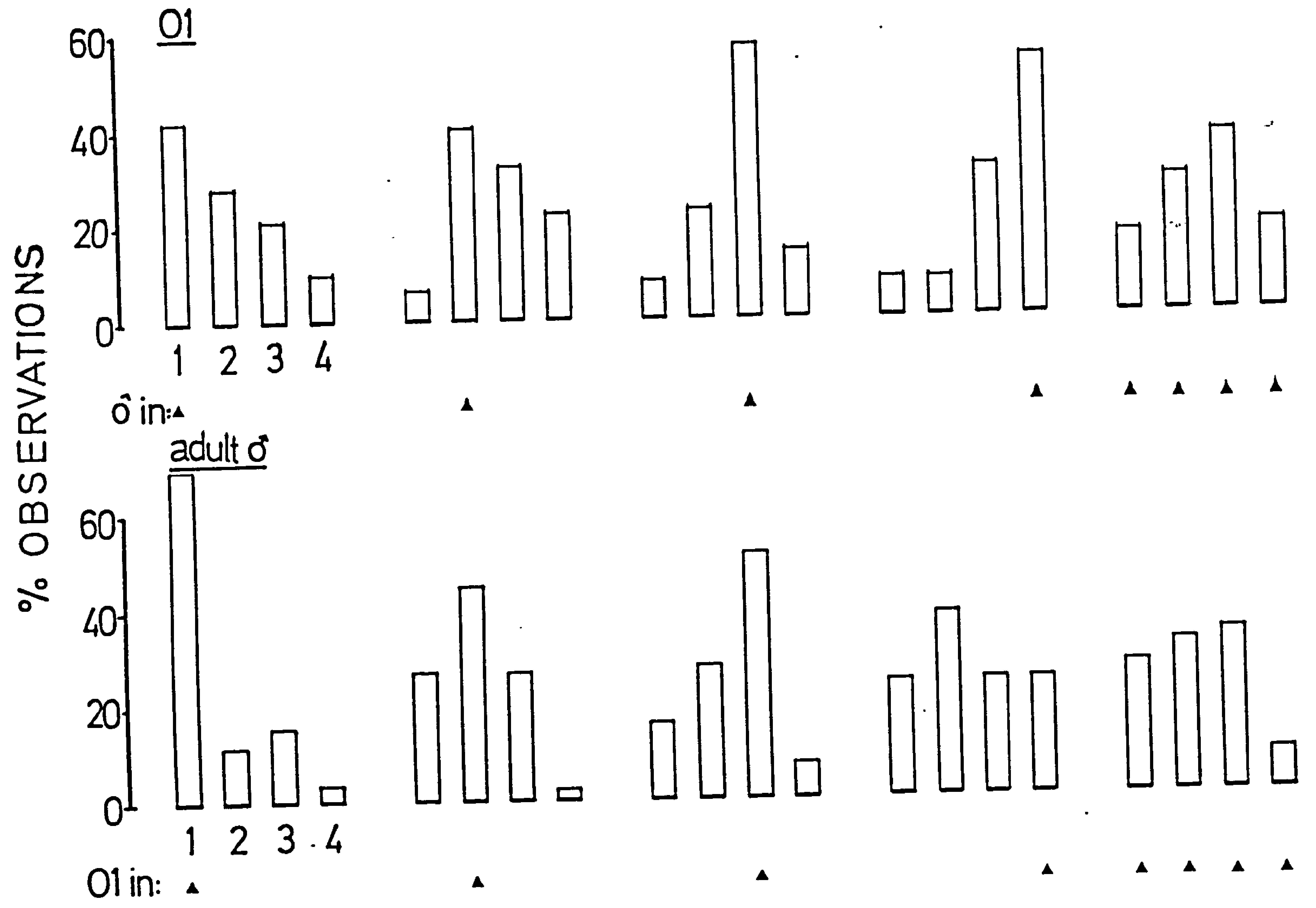

% OBSERVATIONS
O2
60
40
20
0
1
2
3
4
♀ in:▲
adult ♀
60
40
20
0
1
2
3
4
O2 in▲

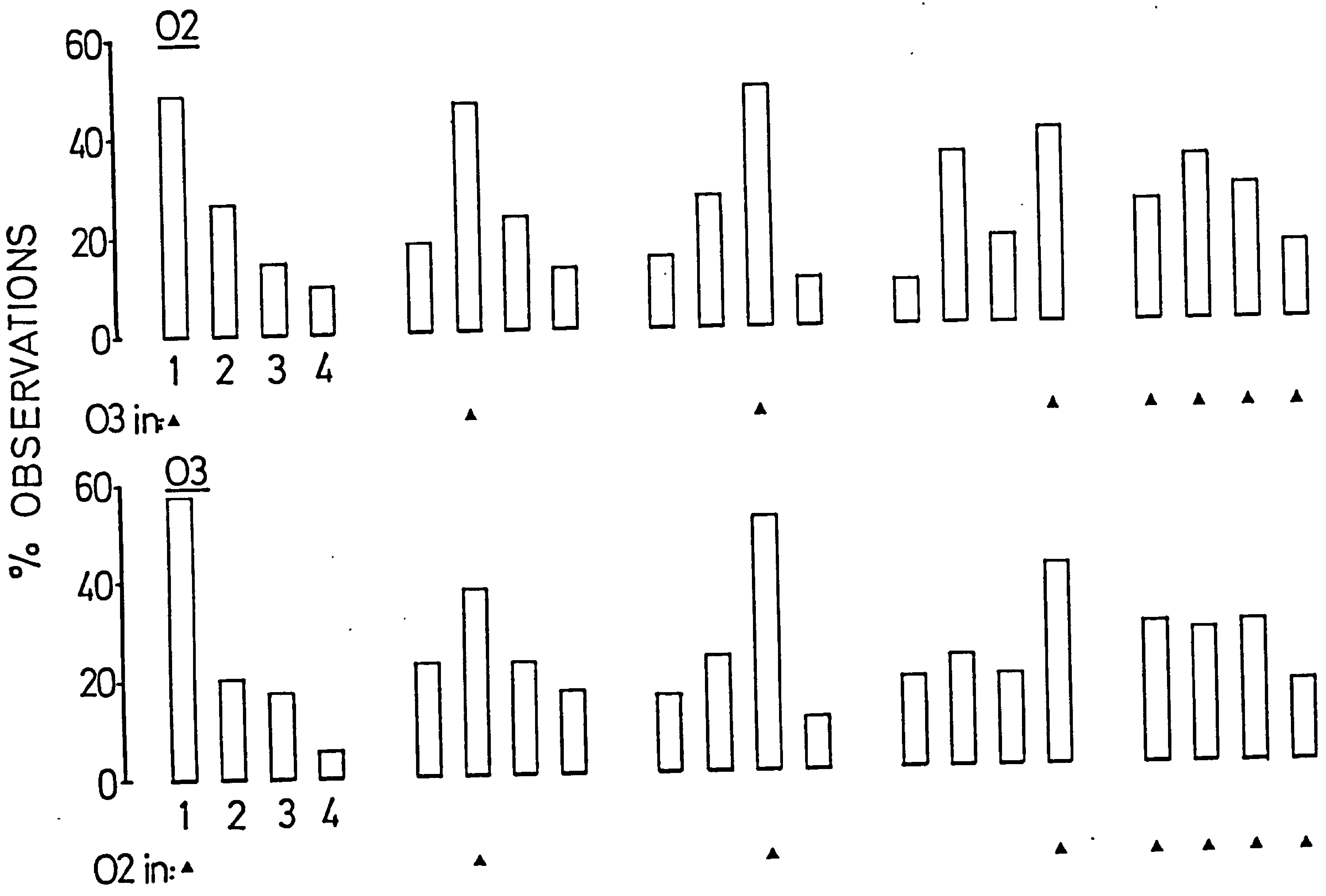


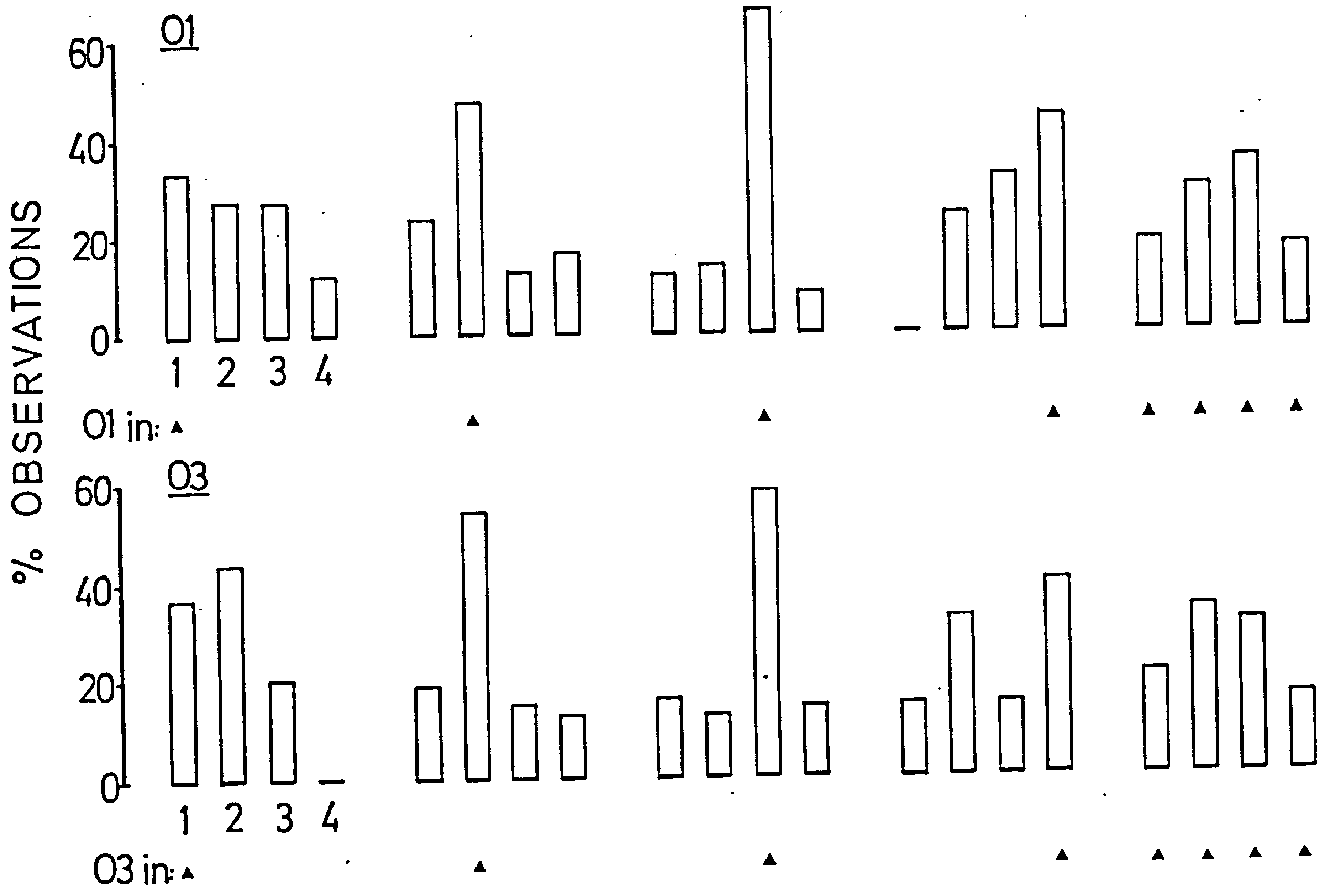
% OBSERVATIONS
O1
60
40
20
0
1
2
3
4
♀ in:
adult ♀
60
40
20
0
1
2
3
4
O1 in:

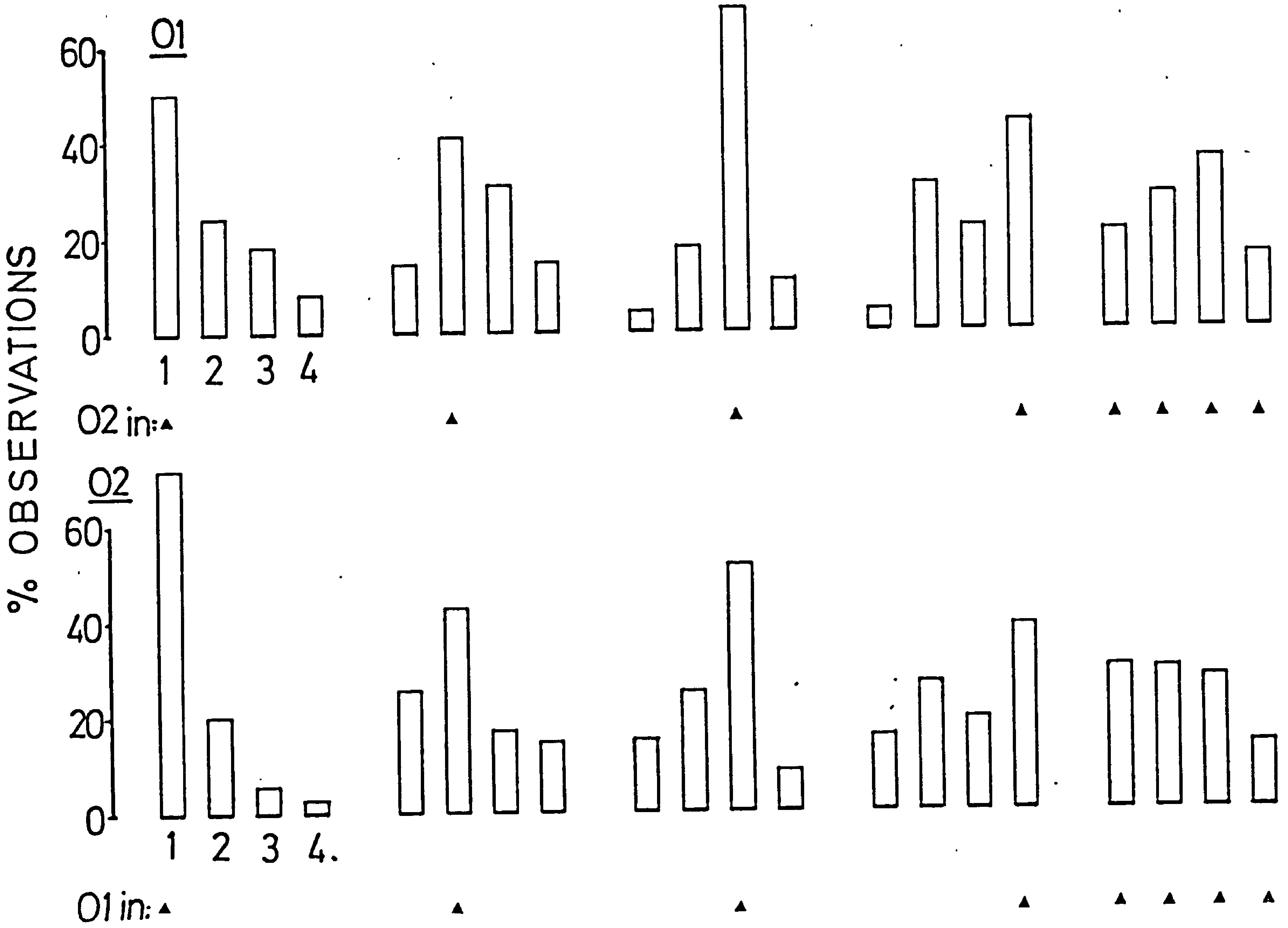

% OBSERVATIONS
O3
60
40
20
0
1
2
3
4
♂ in:▲
adult ♂
60
40
20
0
1
2
3
4
O3 in:▲

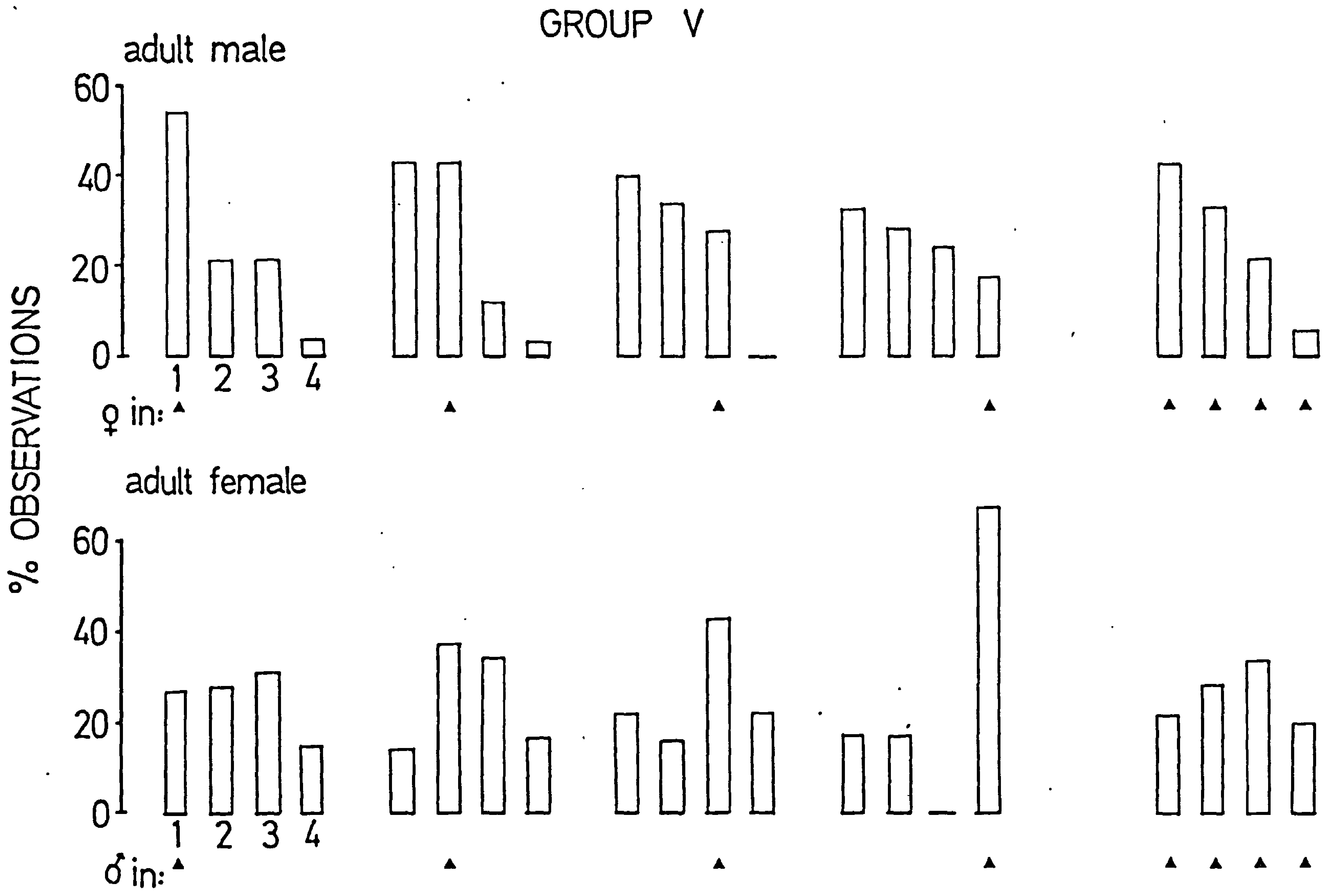

% OBSERVATIONS
O2
60
40
20
0
1
2
3
4
adult ♂: ▲
adult ♂
60
40
20
0
1
2
3
4
O2 in: ▲


% OBSERVATIONS
O1
60
40
20
0
1
2
3
4
♂ in: ▲
▲
▲
▲
▲ ▲ ▲ ▲
adult ♂
60
40
20
0
1
2
3
4
O1 in: ▲
▲
▲
▲
▲ ▲ ▲ ▲


% OBSERVATIONS
O2
60
40
20
0
1
2
3
4
O3 in: ▲
O3
60
40
20
0
1
2
3
4
O2 in: ▲


% OBSERVATIONS
O1
60
40
20
0
1
2
3
4
O1 in: ▲
O3
60
40
20
0
1
2
3
4
O3 in: ▲


% OBSERVATIONS
O1
60
40
20
0
1 2 3 4
O2 in: ▲
O2
60
40
20
0
1 2 3 4.
O1 in: ▲


GROUP V
adult male
adult female
% OBSERVATIONS
60
40
20
0
1
2
3
4
♀ in: ▲
♂ in: ▲

(iii) the O3 individual spent more time in the canopy top when the adult female was in the 'middle canopy' than when she was herself in the canopy top.

7.2. Canopy level asynchrony between individuals.

Although overt differences were not immediately obvious in Group P, cases of relative asynchrony of canopy level were considered between pairs of *Indri*. The proportions of time that one individual was lower or higher in the canopy than a selected partner were related to their situation in the 'same' or 'separate' trees. Due to sample size shortcomings each pair of animals could not be tested against every other pair, but the percentage of occasions (when two animals were seen together) that each was higher than the other, was calculated (Table5.10).

7.2.1. Associations between 2 animals.

For all pairings in Group P, no obvious difference existed between individuals or within individuals (according to whether they were in the same or different tree from their partner) in the proportion of the time they were the 'highest' (Table 5.10).

Although no statistical confirmation is available, both the adult female and juvenile were more often higher than the adult male in both same and separate tree situations (Table 5.10). There were no significant differences in this group for any pairing in tendencies for one individual to remain higher than another simultaneously seen individual (X^2_{1df}(max) = 3.4206, $0.05<p<0.1$).

The adult female in Group V, however, was observed higher than the adult male seven times more frequently when they were in the same tree but only twice as frequently when they were in separate trees. Both results are significant, as is the difference between them (X^2_{1df}= 3.8, p= 0.05) - see Table 5.15 .

7.2.2. Larger associations.

In order to examine the social implications of crowded situations on individuals' relative positions, data were taken where 3, 4 and 5 animals were located in one tree (Table 5.11). Tree size and stability were probably important contributory factors governing the frequency of such associations. The data cannot, therefore, be lumped so as to provide a more satisfactory sample size.

In only one case was there a significant difference between individuals' participation in 3 animal-per-tree aggregations - the adult male being less frequently involved than the juvenile (X^2_{1df}= 10.40, $0.001<p<0.01$).

The proportion of time spent outside the food bearing parts of the trees may have been greater for the 03 individual in large aggregations, but the sample size is small. Consistent differences in progression orders (Chapter 7) and the order of entry into a tree (Chapter 6) in which the whole group fed could have accounted for the variation.

With respect to each other, individuals in 3 animal-per-tree aggregations did not appear to associate in

	Ad♀	Ad♂	03	02	01
UC	0	0	4	1	0
CB	3	2	3	4	4
C	16	16	11	11	14
CT	5	6	6	8	6
%TOP	58	65	46	61	61
%BOT	42	39	54	46	50

(1) 5/tree

	Ad♀	Ad♂	03	02	01
UC	1	4	3	3	0
CB	10	9	3	8	5
C	11	13	9	12	19
CT	3	2	6	4	6
%TOP	24	25	43	26	47
%BOT	40	36	29	30	10
N	25	28	21	27	30

(2) 4/tree

	Ad♀	Ad♂	03	02	01
UC	3	5	5	9	8
CB	10	7	18	12	15
C	20	13	12	13	22
CT	7	2	7	7	8
%TOP	50	1	21	24	32
%BOT	12	30	29	39	24
N	40	27	42	41	53

(3) 3/tree

TABLE 5.11. Individual participation and positions in same-tree aggregations in Group P.

Ad♀	Ad♂	03	02	01
1.8	1.0	0.9	0.9	1.8

TABLE 5.12. Ratio of $\dfrac{\text{Number records subject was "highest" in tree}}{\text{Number records subject was "lowest" in tree}}$ in Group P

DYAD	OBSERVED	EXPECTED*
Ad♀ + Ad♂	9	13.1
+ 03	22	20.5
+ 02	18	19.6
+ 01	31	26.3
Ad♂ + 03	14	14.7
+ 02	12	14.4
+ 01	18	17.8
03 + 02	20	21.0
+ 01	27	27.6
02 + 01	31	27.0
TOTAL	202	202

*Expected value of 'x' and 'y' individuals' association frequency given by:

$$\frac{2n_x \cdot n_y}{(\Sigma n)-n_x}$$

assuming random aggregation but allowing for individual participation variation.

TABLE 5.13. Observed and expected dyadic associations in 3 animal/tree aggregations in Group P.

anything but a random pattern (Table 5.11).

The proportion of records in which each individual was (i) the highest and (ii) the lowest animal in a tree were examined. A ratio of the relative number of records each individual was highest or equal highest in the trees occupied by at least 2 other individuals compared to instances when they were lowest or equal lowest, was calculated (Table 5.12). This ratio clearly separated the adult female and juvenile from the rest of the group.

8. SUMMARY OF SOCIAL INFLUENCES ON LOCAL SPACING

From association frequencies between individuals (1) in the same tree and (2) irrespective of the tree, 4 types of spacing relationship between individuals were proposed. The closest relationship was exhibited by the Group P adult female with her youngest offspring (O1). The relationship between the adults of the two groups differed in that although the adults of Group V remained closer overall, they were less frequently found in the same tree than the adults of Group P.

The social effects of other individuals were more closely investigated by recording the relative positions ('higher' or 'lower') of pairs of animals. Although no significant differences within Group P could be confirmed, the adult female of Group V was much more frequently found higher than the adult male in the same tree. When these two animals were situated in separate trees, the same relationship existed although the difference was significantly reduced.

In situations where members of Group P were largely or completely restricted to a single tree, the adult female and juvenile seemed to spend more time at the top and less time at the bottom of the tree compared to other animals. This difference, however, was not statistically significant.

9. LOCAL SPACING WITHIN CANOPY LEVELS

At 30-minute intervals the heights of all visible individuals were recorded. Height estimates were required in order to examine social aspects of relative vertical displacement within canopy level categories.

9.1. Methods.

Individuals' heights were recorded by reference to a single animal. The altitude of one individual, generally the lowest, was evaluated and all other animals seen allocated additional height increments. In this way the emphasis was placed on individual differences in height rather than absolute values. These values, however, were repeatedly checked using a Zeiss altimeter in monthly practice sessions.

Between 300 and 450 records of height were collected for each individual throughout the year.

An animal's height was less easily determined than its canopy position. Four or five animals in one tree might easily be allocated to a canopy level, but their heights would be often difficult to perceive if the observer was situated at the foot of the tree. For this reason, the percentage of time that each animal was in the same tree as another was underestimated by selecting IARs when height was recorded.

Other biases were complex in nature and immeasurable. It was by no means consistently true, for example, that higher animals were more difficult to see than lower ones.

9.2. Results.

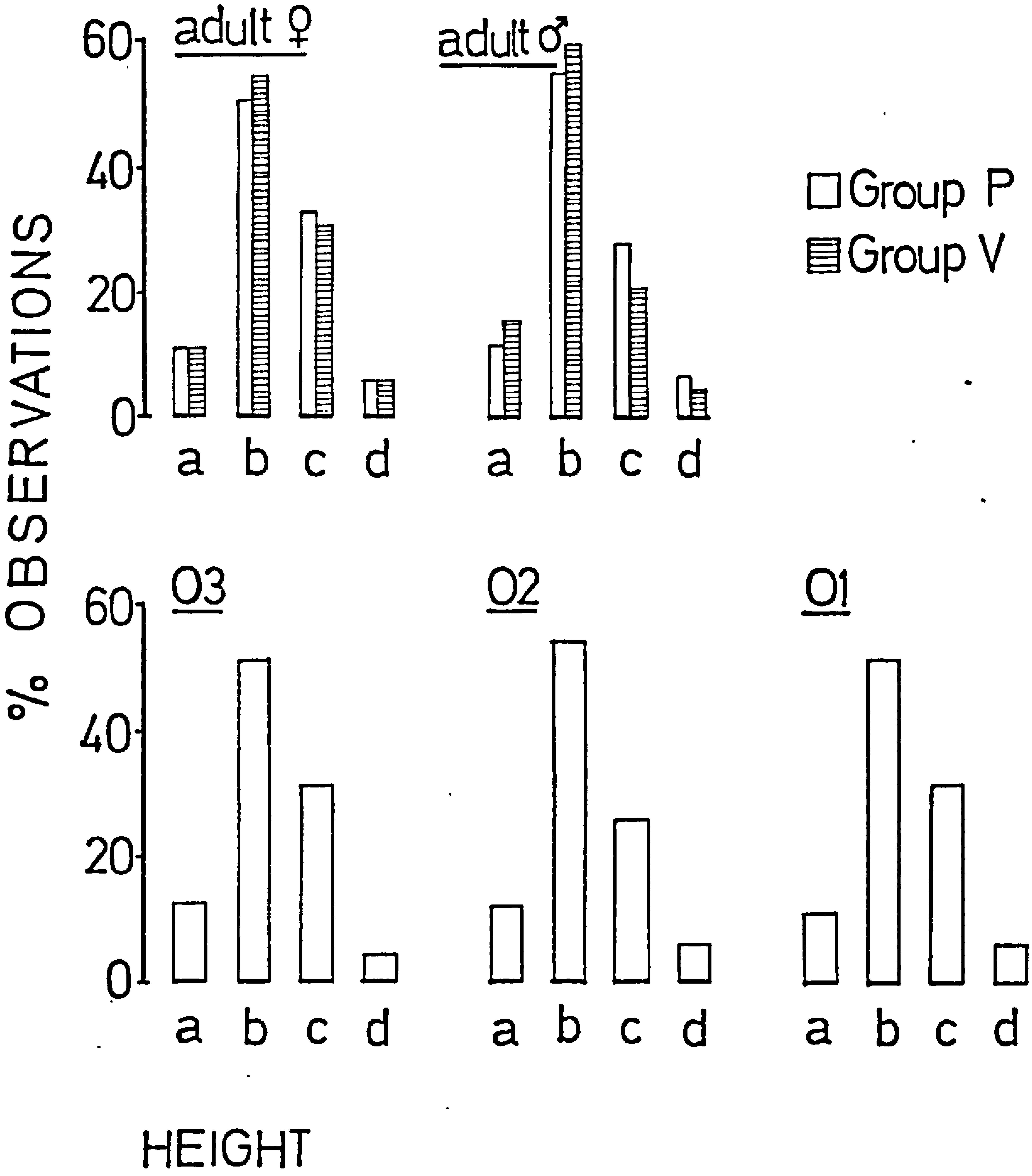
9.2.1. Overall differences in heights between individuals.

Heights were in each case normally distributed and values of 't' were therefore employed to test differences. In Group P only those individuals whose mean heights were least alike were tested (O1 and O2) and as differences proved non-significant ($t=0.847$, $p=0.4$) it was concluded that no substantial inter-individual variation in mean height existed.

A finer examination of individuals' heights (Fig.5.3) was made by comparing the proportions of recorded heights that fell into each of 4 categories: category 'a' (0-8 ms), 'b' (8-16 ms), 'c' (16-24 ms) and 'd' (24 + ms). In no category were significant differences encountered between individuals of Group P (X^2 tests$_{(4df)}$: 'a'$X^2 = 0.6610$, $0.95<p<0.98$; 'b'$X^2 = 2.0286$, $0.7<p<0.8$; 'c'$X^2 = 5.0938$, $0.2<p<0.3$; 'd'$X^2 = 1.7953$, $0.7<p<0.8$). There were no significant differences found within pairs of animals within each category.

In Group V the mean height of the adult male was inferior to that of the adult female ($t=3.058$, $0.001<p<0.01$).

Figure 5.3 The proportion of time spent by each individual in each group in each of 4 categories of height: 'a' (0-8 metres), 'b' (8-16 metres), 'c' (16-24 metres) and 'd' (24+ metres).



% OBSERVATIONS
adult ♀
adult ♂
□ Group P
▤ Group V
O3
O2
O1
0
20
40
60
a
b
c
d
HEIGHT

The adult male spent significantly longer than the adult female in category 'a' (X^2_{1df}= 5.7748, $0.02<p<0.01$) and significantly less time in category 'c' (X^2= 11.1543, $p<0.001$).

The adult male of Group V remained on average lower than every member of Group P (t_{min} = 2.122, $0.03<p<0.04$).

9.2.2. Simultaneous records of individual heights.

(i) All trees.

For each pair of animals the higher individual was noted at each point sample (Table 5.14). Those individuals which spent a greater proportion of time higher than others also spent on average, less time lower. Animals were seen, therefore, at the same height as others with equal frequencies.

The adult male of Group P was found to spend significantly more time lower than any other animal, compared with all other group members except O2 (X^2_{1df}:
Ad♀ X^2= 17.07, $p<0.001$; O3 X^2 = 7.26, $0.001<p<0.01$;
O1 X^2 = 13.74, $p<0.001$).

When each pair in Group P was considered separately 3 of the 5 significant differences found involved the adult male. This individual was significantly lower than the adult female (X^2 = 7.81, $0.001<p<0.01$), O2 (X^2 = 7.98, $0.001<p<0.01$) and O1 (X^2 = 20.387, $p<0.001$) when seen in their company. In addition O2 remained lower than both the adult female (X^2 = 5.854, $0.01<p<0.05$) and O1 (X^2 = 10.460, $p<0.001$) when he was seen with each of them.

The adult female in Group V was three times as often

	IND	% HIGHER	% SAME	% LOWER
Group P	Ad♀	37.8	32.8	29.4
	Ad♂	27.0	29.5	43.5
	03	34.1	30.5	35.4
	02	31.7	33.1	35.2
	01	36.4	36.4	27.2
Group V	Ad♀	62.7	15.6	21.7
	Ad♂	21.7	15.6	62.7

(1) % of individuals' records of relative height

% HIGH	% SAME	% LOWER
23.7	21.2	18.5
14.5	16.3	23.4
19.1	17.6	19.8
17.8	19.2	19.8
24.9	25.7	18.5

(2) % of groups' records of relative height

TABLE 5.14. Overall measures of individuals' relative heights.

	Mode	SAME tree			SEPARATE trees		
		N	n higher	% higher	N	n higher	% higher
Group P	Ad♀	331	109	32.9	365	154	42.2
	Ad♂	264	56	21.2	333	105	31.5
	03	329	88	26.8	293	125	42.7
	02	326	84	25.7	299	114	38.2
	01	394	107	27.2	366	170	46.4
Group V	Ad♀	81	50	61.7	192	121	63.0
	Ad♂	81	10	12.3	192	49	25.6

TABLE 5.15. Individuals' overall proportion of "higher" records in different tree modes.

higher than the adult male when they were seen together, a difference far greater than for any two animals in Group P.

In both groups, therefore, the adult males were lower than others seen to be near them. In Group P there was no overall difference in mean or categorised heights between individuals suggesting that the adult male avoided higher positions only when he was near to other individuals. In Group V the adult male was the lower individual so frequently that the difference is also represented in average height measurements.

Both the adult female and the juvenile (O1) appeared to affect the heights taken by O2. In both groups the adult females were, on average, higher than other individuals.

(ii) Individuals in the same tree.

A test was conducted to compare the proportions of time that individuals were higher than others when these were situated in (i) the same, and (ii) separate trees (Table 5.15). For each pair of animals the tendency for one individual to be higher than another was independent of their situation in the same or separate trees (X^2_{1df}(max) = 1.67, $0.1<p<0.2$). Only the case of the juvenile, who was higher than the adult male (X^2_{1df} = 3.89; $p = 0.5$) in the same tree constituted a significant difference.

The adult female of Group V was 5 times more often higher than the adult male when they were together in a tree. This difference was halved when they were in separate trees.

9.2.3. Large aggregations in a tree.

(i) Five animals per tree.

Very few records exist where all animals' heights could be simultaneously recorded in the same tree. A high degree of height synchrony was observed in these situations, however, and the considerable size of trees containing all five animals at one time allowed inter-individual distances of up to 60 feet to be maintained. If food was scarce in such trees, often due to frequent visits from the group over short periods of time, aggressive interactions and the degree of height asynchrony increased.

(ii) Four animals per tree.

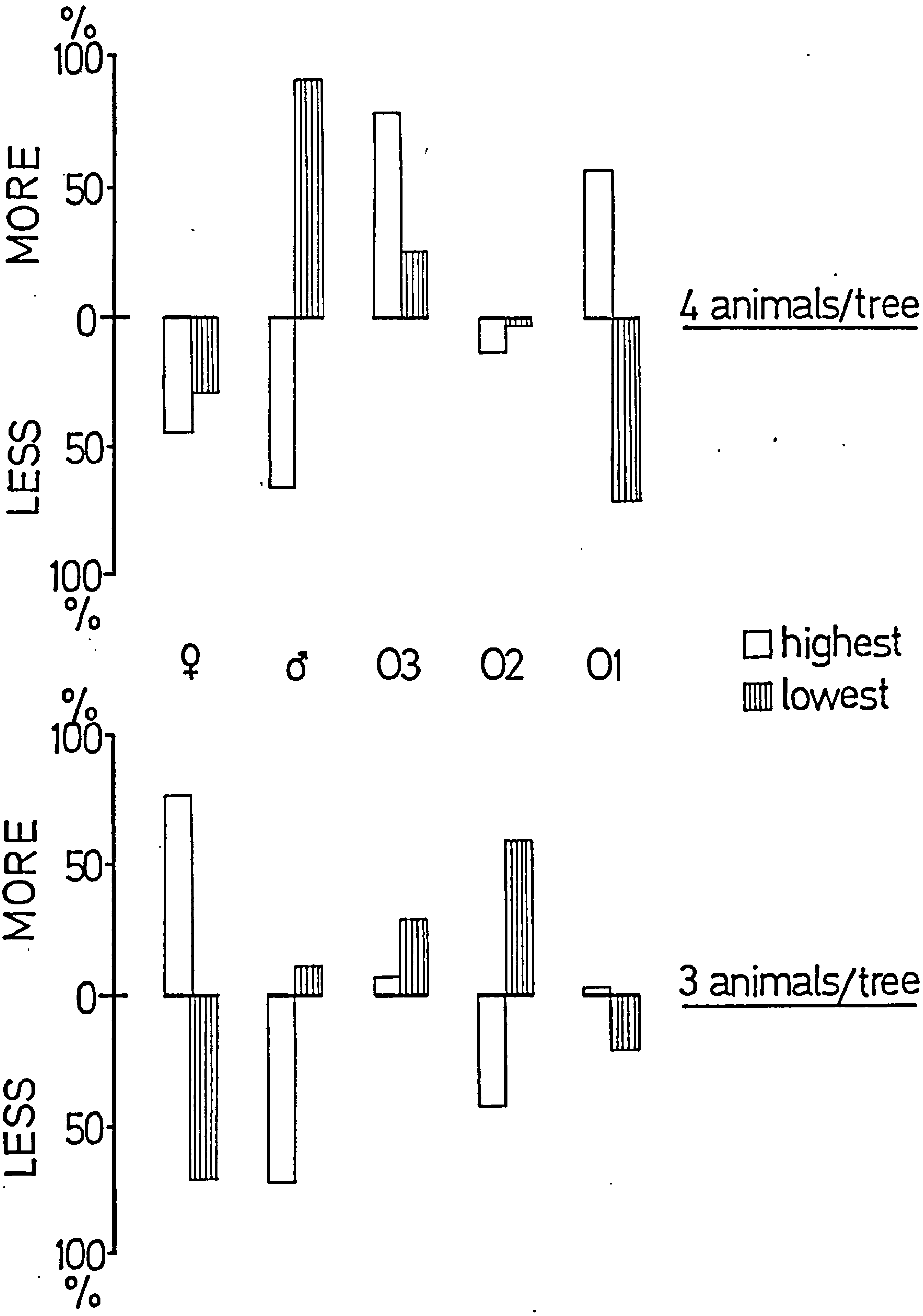
Height records from 30-minute spaced point samples were also infrequent for instances of 4 animals in a tree (n=58). Observations were plotted as percentages of those values expected if animals had positioned themselves vertically in an equal and independent fashion (Fig.5.4).

The only two consistent differences showed that:

(i) the adult male spent more time than expected lowest in the tree and less time than expected highest in the tree, and,

(ii) the juvenile spent more time than expected highest in the tree and less time than expected lowest in the tree.

<u>Figure 5.4</u> The relative height of each Group P individual when situated in a tree containing (1) 4 and (2) 3 animals. Observations are plotted as a % more or less than expected had relative heights of individuals in such situations been random.


%
100
MORE
50
0
LESS
50
100
%
4 animals/tree
♀
♂
O3
O2
O1
☐ highest
▥ lowest
%
100
MORE
50
0
LESS
50
100
%
3 animals/tree

(iii) Three animals per tree.

As for the analysis performed with canopy level data, the adult female figures prominently as the 'highest' individual in 3 animal-per-tree associations, and was rarely found to be the lowest (Figure 5.4). The adult male was rarely highest and the O2 individual was also placed relatively low on average. Small sample sizes and differences in travel order (see Chapters 6 & 7) may have affected these results.

10. SUMMARY OF THE DIFFERENCES BETWEEN INDIVIDUALS' HEIGHTS

Small differences between individuals' heights might have social significance but remain concealed in an analysis of canopy categories. A search was therefore made for differences of heights within canopy divisions between pairs of individuals.

Mean heights did not differ between individuals of Group P, but the Group V adult male remained lower than both the adult female and all members of Group P.

When seen together, the Group P adult male was more often lower than every other group member except the O2 individual. The Group V adult male's height only rarely exceeded that of the adult female.

Relative canopy positions of pairs of animals in the same tree failed to show for Group P any significant differences (see Section 6.2.2). This was thought likely to have been a Type II error resulting from limitations in the size of the sample. As no significant differences save one were located for the heights of individuals in the same tree, and no significant differences existed between individuals' height relationships in the same and separate trees, it is concluded that no measurable differences occurred in this group between individuals' heights within categories. Verification of this finding requires checking that each individual used trees of equal height, but no relevant data were collected on tree height in the present study.

In Group V the great difference found between the adults' relative vertical positions was verified from records of height.

Height measurements were unable to provide statistical support for suggested differences found between individuals' relative positions in cases where many animals were in a single tree.

11. DISCUSSION

11.1. Introduction.

Measures of canopy use by individual Indri at Analamazoatra were rich in differences both between groups and amongst individuals. The aim of this discussion is, by differentiating between 'distant' and 'proximal' measures, to construct reasonable hypotheses which account for the position of specific individuals in the trees according to the position of other group members. The underlying assumption - that individual Indri, unrestrained by social influences, would choose the same positions on average - is necessary in order to make meaningful statements about the social organisation of spacing.

The choice of a selected position in a tree is considered to be dependent on only two (perhaps not unrelated) factors:

- (i) social restrictions or facilitations, and,
- (ii) different physical capabilities of different individuals.

11.2. Role in Indri groups.

In Group V the adult male could be justifiably labelled 'subordinate' to the adult female. Dominance is not easily defined in *Indri*, as it is in many simian species, by overt social interactions (Rowell 1966). A fundamental property of the relationship between the adults of Group V was its inhibitory effect on social behaviours. A positional relationship, henceforth termed "role", was however evident in this group from very early in the study, and made effectively conspicuous by its absence in Group P (but see below). "Role" occurred when different forest levels were simultaneously occupied by the two adults with a concomitant asynchrony in activity (see Chapter 6). The most common manifestation of role consisted of the female feeding high up in the canopy whilst the male rested low down either in the same tree or in a tree nearby. This configuration (Plate 5.2) was not always present and not invariable, being occasionally 'reversed'. In these cases the female rested low whilst the male fed. Role reversal was, however, relatively infrequent and, when it did occur, it did not persist for long. Four aspects of behaviour suggested that this was more than a simple division of labour (e.g. 'vigilance') within the group:

PLATE 5.2 'Role' configuration in *Indri* Group IV at Vohidrazana. Two individuals (one of which is the adult female), in this group of four animals, are in the canopy, feeding, whilst the adult male rests underneath the canopy.

(i) Agonistic or 'voluntary' displacements, though infrequent, were always unidirectional. They occurred when the male attempted to feed near the female or when the female attempted to feed near the male. In either case it resulted in displacement of the male to a low role position.

(ii) Role reversal occurred only when the female had already fed from a tree, into which the male subsequently moved. The adult male then usually took her exact vacated feeding position i.e. he received second choice at many food sites. The wide distribution of food about the foliage of most trees gave this striking observation a clear social significance. When the adult female rested the adult male was never permitted by her to feed in a food site she had not previously investigated.

(iii) Termination of role by the male sometimes resulted, after a variable resting latency period, in a feeding bout in the same tree as the female but in a situation maximally distant from her. If she moved to his feeding spot he would either take up role again or shift to continue feeding at the other side of the tree. Termination of role by the female normally resulted in her progression to a new, sometimes distant feeding site.

(iv) Look-out roles have been described for adult male Erythrocebus patas (Hall 1965), Cercopithecus aethiops (Gartlan 1968) and Lepilemur mustelinus (Charles-Dominique & Hladik 1971), but the position of these animals is high - presumably to gain a wider field of view. In the rain forest terrestrial predators may be more easily seen from a position underneath the canopy than from above. However, Indri were much more sensitive to large birds of prey than ground-living animals (although these were probably frightened off by my presence).

In Group P some observations of role were recorded. These were less frequent and less obvious than in Group V and generally resulted from aggressive displacements by either adult of O3 or O2 when they were in feeding positions:

"4/5/1973 1331...The adult female and O1 are feeding together. O2 rests in the lower parts of the same tree. Both feeding animals leave and O2 goes to feed in their spot..."

"28/6/1973 1255...O1 moves into a 'middle canopy' position from 'canopy bottom' in order to feed, and the adult male immediately descends into role position. O1 was at no point closer than 8 metres from him..."

"23/11/1972 0955...O3 starts to feed. The adult male moves nearer to O3 who descends 1 metre. The adult male then aggressively displaces O3 who descends 3 more metres. The adult male and O3 rest high and low respectively in the same tree. The adult male begins to feed..."

Displacement 'dominance' in this group was necessarily more complex than in Group V, but the adult female and juvenile or infant were never displaced in either group.

Differences in canopy level utilisation between groups have been shown to be attributable to specific individual differences. The spatial relationships between the adults of each group, for example, were different:

(i) The adults of Group V were seen together more often than the adults of Group P but spent relatively less of that time in the same tree.

(ii) Both adult males spent more time lower in the trees than other individuals. The preference for low positions was much more marked in the Group V adult male than the Group P adult male.

(iii) Compared to Group P the adult female of Group V was more often higher than the adult male in the same tree than when they were in separate trees.

(iv) Compared to Group P the 'terminal' parts of the canopies were avoided by Group V. The difference between the two groups in this measure was entirely due to the reluctance of the adult female of Group V to enter these positions.

As only two groups of Indri were studied it is impossible to separate normal behavioural variability between groups from differences deriving from group size or complement. Two conflicting expressions, however, appeared to dominate interactions and the organisation of social behaviour in Group V:

(i) the adult female's clear social priority in feeding situations, and,

(ii) the male's subordinance coupled with a balancing motivation to remain near the female.

The result of the equilibrium between these expressions of individuality was a vertical differentiation of position - the female often situated in the food and the male positioned below it. Inhibition of the adult male's feeding activities by the adult female (see Chapter 6) was also observed in Group P (Analamazoatra) and Group IV (Vohidrazana), and "role" configurations were seen in at least 6 Indri groups during the course of the study. As a result of these observations it is considered very unlikely that the 'dominating' relationship between the adult female and the adult male in the two study groups was peculiar to these groups.

Neither the growth of the infant in Group V nor the arrival of an infant in Group IV in May 1973 obviously influenced the spatial relationship of the adult pair.

From an early age infants practiced moving and jumping in the canopy (see Chapter 10). They were at this time still suckling and being transported by the mother. At one critical stage the infant was refused transportation for all but the most difficult leaps. Mistakes at these times resulted in unbroken falls of up to 15 metres. The falls were frequent, 1-3 times per day, and left the animal in a dazed semi-conscious state. The female never retrieved the fallen infant. Falls by other animals were rare and generally occurred under two circumstances:

(i) Mid-air collisions when animals leapt simultaneously for the same support at the same time, and,

(ii) Branch breakage at structurally weak points of the tree. Weak points occur in terminal foliage or branches of small diameter.

It is likely therefore that terminal canopy positions were avoided by the Group V adult female so as to protect the infant (who always remained very close to her) from such contingencies.

11.3. Ecological and individual variation within groups.

Differences in canopy utilisation, analysed for each pair of animals, throw light on some aspects of spatial relationships within groups.

In Group P the adult male and O3 animals stayed longer in lower parts of the canopies than other individuals. The highest parts were occupied more often by O2 and O1 whilst the adult female took intermediary positions.

For the activity of 'feeding' the conclusions are essentially similar - the adult male and O3 remaining distinct from others in the group. Between individuals of different groups, the main feeding canopy utilisation difference was the marked preference for feeding on non-supporting vegetation low in the forest. Falls by the infant in these positions were without consequence, but this behaviour may have developed for quite different reasons. By feeding in this way Indri could obtain a large quantity of the young leaves of saplings - a source of concentrated protein (Hladik et al 1971, see Chapter 6).

It is not, due to the extensive synchrony in canopy positioning and limited differences between individuals, possible to claim the presence of a great ecological differentiation within groups of Indri. Some circumstances arose, however, when some animals were better suited to exploiting a certain source of food than others:

(a) Large trees.

Light animals were noticeably more manoeuvrable and presumably safer in suspended feeding positions (Plate 5.3) than others. This may have accounted for the well-developed preference by O2 for terminal positions. It is impossible to state, however, that food in parts of any large trees was physically unattainable by any individual.

(b) Small trees and saplings.

Small trees and saplings are usually pulled towards a nearby vertical trunk by an animal adopting the 'V.C.L.'[1] posture (Fig. 5.4), but often they are situated beyond the arm's reach and can only be consumed from a position in the plant itself. These positions are most easily taken by light animals. Cases frequently arose where the infant (aged between 9 and 15 months) thus obtained food physically denied the adults.

Noticeable differences also existed in Group P where the juvenile (aged 13-27 months), even when 60-70% the size of the adults, possessed a feeding advantage over the rest of the group. No case was observed where larger Indri fed on food physically beyond the capabilities of smaller group members.

11.4. Spatial relationships in Indri.

By measures of the frequency with which animals were

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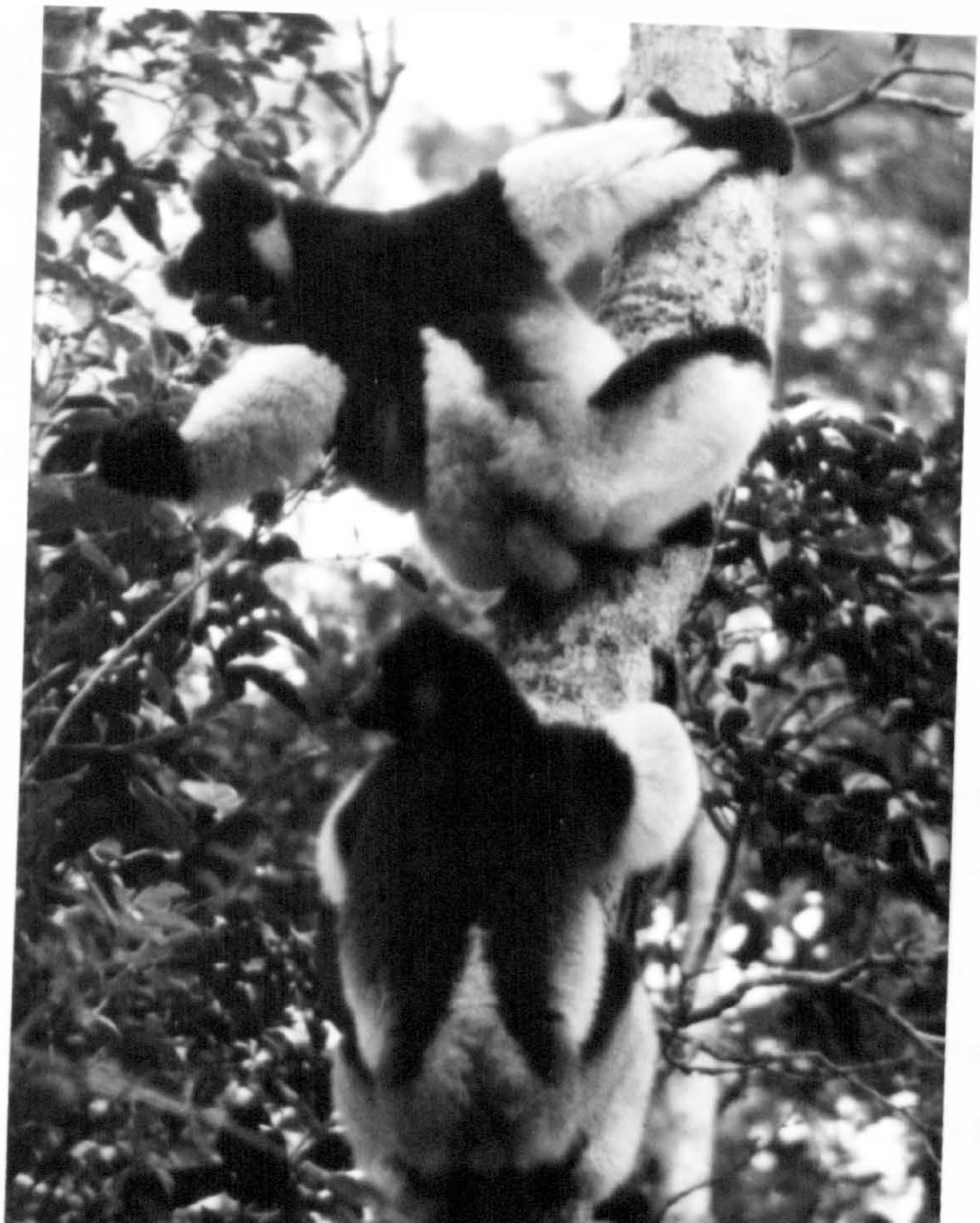
[1] Vertical clinging and leaping posture (Napier and Walker 1967).

PLATE 5.3 *Indri* feeding in a 'terminal canopy' position ('terminal feeding') using a suspended body posture.

PLATE 5.4 Adult female (above) of Group P feeding on a sapling whilst supported in 'clinging' posture on the trunk of an adjacent tree ('feeding on non-supporting vegetation').



(a) seen together and (b) seen together in the same tree, and by comparing their positions in trees relative to others in (a) all cases and (b) the same tree, four types of dyadic spatial relationship have been proposed for Indri. In 'large' aggregations of 4 or 5 animals few spatial differences, beyond individuals' slightly different participation frequencies in such aggregations, were established. For this reason it is considered reasonable to regard the main social effects of spacing to be caused by relationships between two individuals irrespective of the presence or absence of others.

The closest spatial relationship is that of the mother and the youngest offspring. These two animals were the two most often seen together, and when they were together they were the two most often seen in the same tree. They both remained higher than other individuals when they were feeding near to other group members. The spatial relationship between the Group V adult female with her infant/juvenile aged 15 months appeared to be identical to that in Group P when the young offspring was the same age.

In contrast the most distant relationship, between the adult male in Group P and the oldest (male) offspring, O3, was characterised by a low general and intermediary same-tree association score. They appeared to be closest together in situations where overall group cohesion was high i.e. in large feeding trees. Distant relationships of a different kind were found between the adult male with both the adult female and the juvenile. The adult male was quite frequently seen in the same scan as the adult female or juvenile, but rarely occupied the female's tree. When they were found together, however, the adult male was usually lower than both female and juvenile.

Other relationships could be classified into cases where either two individuals were seen often together but rarely in the same tree, or infrequently together and often in the same tree. An example in the former instance is the relationship between the two adults of Group V and, to a lesser extent that between the O3 and adult female of Group P. In Group V a high degree of vertical differentiation was also present and dependent on whether the animals were in the same tree or not. No obvious physical separation of this kind, however, occurred between the O3 and adult female of Group P.

Finally, a low general association and a high same-tree score characterised the relationship between O2 and his group's adult female. It appeared that, as for the adult male and O3 individuals, O2 was attracted to close group configurations. O1, who generally possessed spatial relationships with others similar to those of the adult female (due to the affinity these two animals had for each other), differed in one case. Although the adult female had a rather ambiguous spatial relationship with O2, O1 often remained very close to him (O2) and these two animals, the youngest of the group, played frequently with each other. It follows, therefore, that O1 and O2 were frequently together when the adult female was absent.

It may be useful to speculate on the changes in spatial relationship that may occur as offspring in a group become older. This approach requires O1, O2 and O3 to be considered as typical offspring separated by roughly equal numbers (2 or 3) of years.

At first the infant never leaves the mother. As it achieves locomotor independence and when feeding begins small movements away from the mother occur. A closer relationship with the adult male then develops. Over the second year the juvenile follows the female closely and remains near to her when feeding in the canopies. The increasing affinity between the juvenile and adult male does not result in a closer spatial relationship between the adult male and the adult female. At 5 or 6 years of age the sub-adult is less protected from being displaced by others in feeding trees and enters a confusing stage - being tolerated by the adults on some occasions, yet forced to move away (and downwards) on others. By adulthood, the animal is still clearly spatially closer to the adult female than it is to the adult male. Both the adult-sized offspring and the adult male remain more distant than others, and when they do enter a social feeding situation are similar in their response - remaining consistently lower than others. By this stage the adult-sized offspring can be displacedby any other group member (but see Chapter 8).

12. SUMMARY

1. Numerous differences both within and between groups were found in individuals' use of parts of the trees (1) for all activities and (2) when feeding. The adult females of both groups feed higher in the trees than their adult males. Although differences between males of each group were not marked, the Group V female appeared to choose her feeding positions at least partly for the security of the infant.

2. Measures of the frequency with which pairs of animals were seen together helped to define the 'closeness' of different spatial relationships. Differences were found in the tendency for 2 animals to be in the same tree and their tendency to be seen together by the observer. In both groups the adult male was more often seen at lower canopy levels than the adult female. In Group V the tendency for the adult male to take lower canopy levels varied according to whether both adults were in the same or separate trees. This was not the case for Group P.

3. Only the adult male of Group V was consistently at a lower height than other individuals. When seen with others, however, both males took relatively low heights in the forest. Analysis of relative heights did not reveal social influences on positions in trees other than those already found between canopy levels.

4. The dominance of female Indri is effective in keeping the adult males out of the canopy or in positions of poor feeding potential. Light,young animals can profit from food in structurally weak parts of the trees and some intra-group ecological resource partitioning therefore occurs.

CHAPTER 6

Feeding Behaviour

Successful feeding behaviour by members of a primate group requires every individual to obtain sufficient quantities of the right food. The relatively high frequencies of aggressive interactions occurring in feeding contexts (Chapter 8 , Richard 1973) suggest that this potentially competitive situation is likely to contain important information about the nature of social relationships and, therefore, social structure. In the following chapter feeding behaviour is described in terms of individual (nutritive) and social (non-nutritive) requirements.

1. FEEDING TECHNIQUES

1.1. Introduction.

Foliage, flowers and fruit were generally consumed from branches pulled towards the mouth. Small fruit were picked by mouth and often gnawed out of the clenched hand, which thus acted as restrainer and support. Large fruit were bitten from their stalks, transferred to the hand and eaten after the animal had moved to a secure position in the food tree.

The major source of fruit during the study period (consisting of species of the laurel family) were approximately spherical or oval and the size of a large grape. The endosperm of these fruit, when unripe, was scooped out using the dental "comb" (the prominent battery of specialised teeth in the lower jaw (Plate 6.1) as a sharp-edged spoon[1]. Later, the thin pericarps of the mature fruit were gnawed off the hard underlying seed. Before being dropped to the ground these fruit would often be crushed - apparently in order to taste the strong aromatic juices in the kernel.

Mature leaves of rain forest vegetation are thick and rigid and were eaten in bites from the side or apex. The majority of consumed foliage, however, was young, flexible and small and could be clipped off from the stalks - several leaves at a time - and drawn continuously into the mouth whilst chewing and swallowing.

1.2. Feeding postures.

Indri profit from the high rates of leaf production in young trees by spending a large proportion of their time feeding on sapling vegetation. Although saplings are unable to support the 10-15 kilograms that adults weigh , Indri obtain food by pulling them towards the large vertical trunk of another tree from which they can feed, in the VCL posture[2], for several minutes (Plate 5.4). Many of the flowers and fruits of cauliflorous species could only be fed on from these postures.

Fruit and young leaves were often situated on the terminal parts of trees' foliage and their consumption involved one of two postures:

(i) Supported body extension (Plate 6.2); the animal lies on top of a thin horizontal branch, thus supporting

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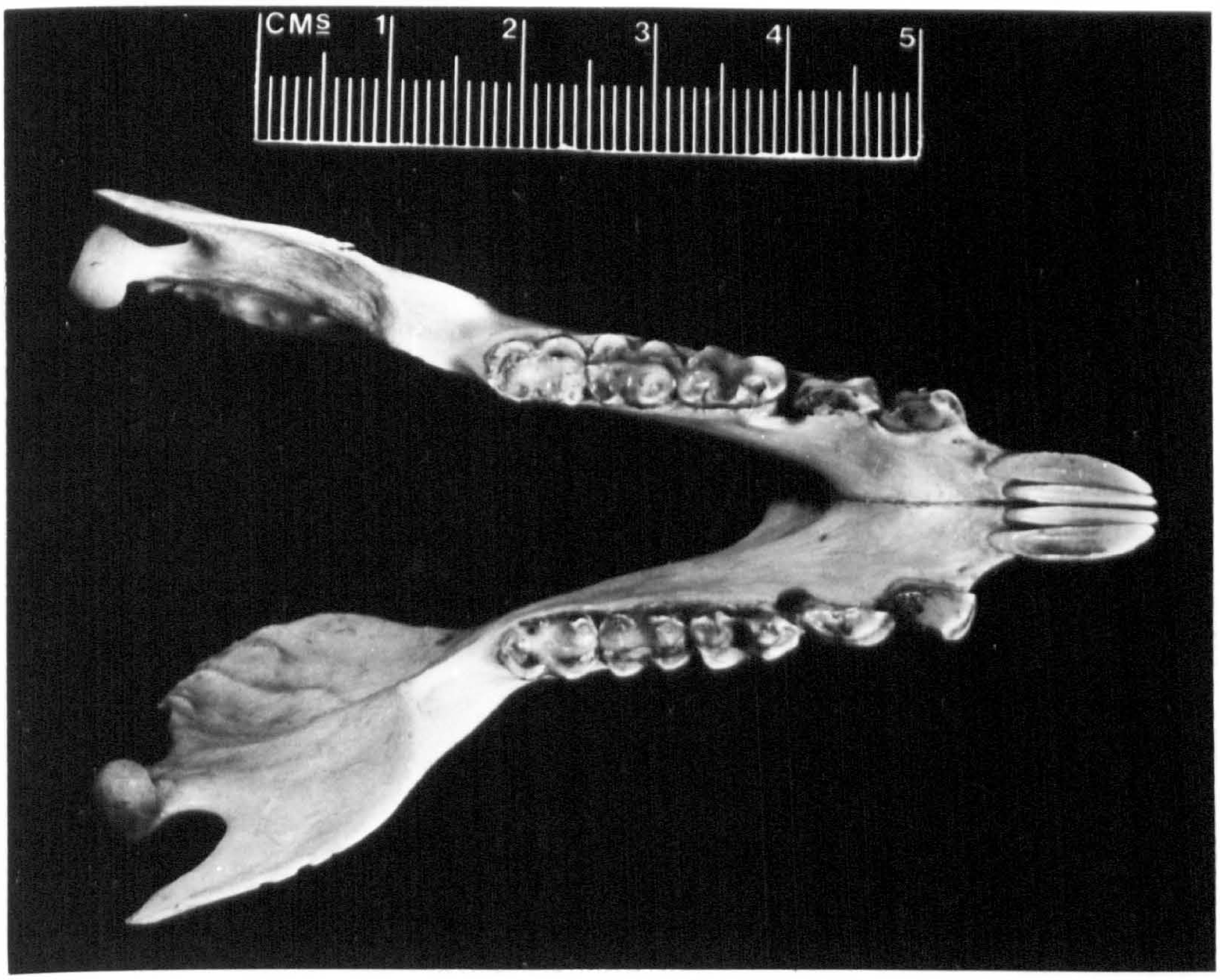
[1] see Appendix 3.

[2] The VCL posture is the body position of Indri when clinging to a vertical trunk, without pelvic support, before and after a leap (see Chapter7).

PLATE 6.1 *Indri* mandible showing the spoon-like 'tooth-comb' at the anterior end used by *Indri* to scoop out the unripe seeds of some species of fruit.


CMS
1
2
3
4
5

both pelvic and dorsal parts of the body; the feet usually clasp vertical trunks or branches;

(ii) Suspended body extension (Plate 5.3); The body is slung under a single, horizontal support to which it is held by both feet and (usually) one arm.

Both postures spread the animals's weight maximally over the supported area. Unlike *Hylobates* (Grand 1972) terminal feeding by *Indri* does not alter the position of the food relative to the hand. Suspended feeding by gibbons, according to Grand, is achieved by a single-arm support, the centre of gravity passing vertically down the body of the animal. A very similar posture is taken by *Ateles* and *Alouatta*, where the prehensile tail alone suspends the animal from a horizontal branch (Carpenter & Durham 1969). Even if *Indri* were physically capable of maintaining such postures their greater weight requires them to place the centre of gravity nearer the vertical trunk.

Foods situated centrally in the trees were consumed from sitting positions on horizontal boughs or branches (Plate 6.3).

1.3. Foraging behaviour.

Indri were seen to look at food, often from considerable distances, and appeared to choose an initial feeding spot before entering a tree. Once there the animal would park itself in a suitable posture and feed continuously for some minutes. Often all the available food was consumed before the animal shifted to a different part of the tree.

PLATE 6.2 'Supported body extension' feeding posture in *Indri*, used for feeding on some foods situated at the edge of the canopy.

PLATE 6.3 'Sitting' feeding posture in *Indri*, used for feeding on foods more centrally situated in the canopy.

Indri would sometimes peer at food in another tree, moving the head slightly as though a better view was obtained by so doing. Close or manual examination of food was not observed, however, and no clear criteria could be defined by which 'foraging' could be recognised as a discrete activity. Richard (1973) concluded similarly in her study on *Propithecus verreauxi*.

1.4. Individual variation in feeding techniques.

Indri use a variety of methods for getting food into the mouth, some of which are consistently peculiar to specific individuals. The function and consequences of this variability are not understood and its effect on feeding rate was not established.

On several occasions animals were seen to feed differently on the same type of food and differences in the method of feeding could not then be attributed to the different structure of the foods e.g. " .... the two adults of Group V feed together on *Tambourissa* sp. leaves. They are both eating large, young adult leaves. The adult female holds a clump of leaves near her face by pulling a nearby branch and feeds by working her way from the apex to the attached stalk in 2-4 bites whilst the adult male folds the base of the leaf, near the stalk, and consumes the leaf anteriorwards as a sandwich. It is not possible to clearly decide which method offers the fastest rate of consumption ...."

One feeding method was observed only in the Group V adult female: " .... a leaf was detached from the branch and held in the front of the mouth, at the posterior end, and eaten in bites along one longitudinal half. When the apex of the leaf was reached the tip was revolved and the opposite half similarly consumed ....". A slight variation on this feeding technique was also demonstrated by this individual .. ".... a leaf was held by the base whilst it was still attached to the tree, a strip up to the central vein being torn off towards the leaf tip before it was eaten ...." Patterns of feeding only shown by the adult female were not copied by the infant of that group.

These feeding methods, which were mostly adopted when feeding on large, wide leaves, varied according to the maturity of the foliage. Mature leaves of evergreen vegetation are structurally rigid whilst young leaves are typically flexible. Trees with a new flush of leaves have small, erect foliage that is easily eaten but as the leaves enlarge with growth they hang limply and present problems for Indri which feed normally without using their hands.

On at least one occasion, however, leaves were picked by hand. The O2 individual, having been aggressively displaced from a feeding position by the adult female (Group P), moved to an adjacent tree and picked the foliage from his former food tree. In this instance it was impossible for O2 to return to the tree without approaching the animal which had displaced him. There may, therefore, be social constraints on the techniques of feeding in Indri, and although this was never seen on other occasions, hands could be used to obtain food directly.

2. THE TIME SPENT FEEDING

In this section the amount of time spent feeding by groups and individuals is represented by the proportion of feeding records in the data. Where variation in parameters of the amount of time spent feeding is considered between groups, proportionate measures are usually converted into absolute measures[1]. Comparison of food part consumption by members of each group, however, located only differences where Group V fed proportionately more than Group P (see Section 2.4). As the time over which Group V fed was greater than that of Group P, proportionate differences could only underestimate absolute differences and conversion is therefore unnecessary.

2.1. Overall time spent feeding by study groups.

The relative proportions of the activity period spent feeding was 39.2% for Group P and 36.6% for Group V. As Group V were consistently active for a longer period of time each day they in fact spent more time feeding than Group P. If the recorded proportion of time that each group spent feeding daily was representative of the whole day, Group V fed more than Group P for a mean of 4.9% of Group P's feeding records.

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[1] by estimating the total number of each group's feeding records were the behaviour of animals out of sight similar to behaviour when sighted (see Chapter 2).

2.2. Seasonal variation.

The percentage of each group's activity period devoted to feeding varied from 30% to 60% throughout the year. The data were insufficiently precise to permit an examination of daily changes of this parameter within Circuits, but the impression gained was of little or no variability.

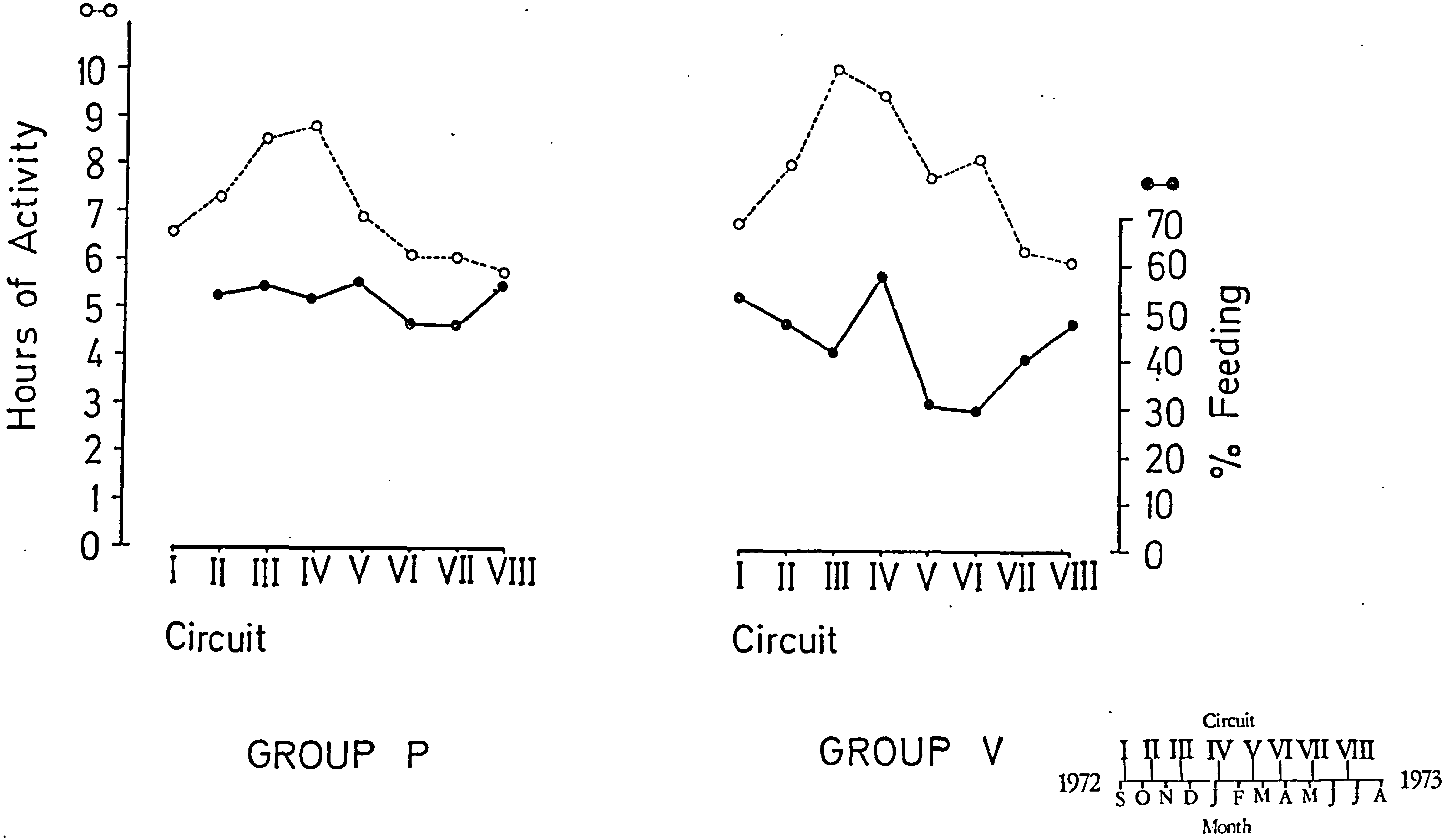
When the period of activity increased during the long summer days the proportion of time spent feeding by Group P remained relatively stable (Figure 6.1) and the real time spent feeding thus increased. For Group P the proportion of time spent feeding during Circuits VI and VII (equivalent to the austral mid-winter) was significantly less than at other times of the year (both Circuits: $0.01<p<0.05$). Compared to other months, during these two Circuits the least fruit was consumed (see Section 2.4.2.).

For Group V feeding was more variable (Figure 6.1), relating presumably to non-seasonal influences. Ten significant differences between Circuits in the proportion of the activity period spent feeding were found, five of which focused on the poor levels of feeding activity exhibited by the group during Circuit V.

2.3. Temporal distribution of feeding.

Indri first show signs of activity between 2-3 hours after dawn and finally take up sleeping positions at a similar interval before dusk. The total period of

Figure 6.1 Seasonal variation in the duration of the activity and the proportion of time spent feeding by each study group at Analamazoatra.



Hours of Activity
0
1
2
3
4
5
6
7
8
9
10
I
II
III
IV
V
VI
VII
VIII
Circuit
GROUP P
I
II
III
IV
V
VI
VII
VIII
Circuit
% Feeding
0
10
20
30
40
50
60
70
GROUP V
Circuit
I II III IV V VI VII VIII
1972
S O N D J F M A M J J A
1973
Month

activity each day can last as little as 5 (mid-winter) or as long as 11 (mid-summer) hours and is sometimes considerably shortened by wet, cold weather conditions. Within this period Indri gradually build up the intensity of feeding to peak at about midday or shortly after (Figure 6.2). Temporary social sessions of 'calling', defaecation and, for Group V, suckling activities were sufficiently variable in their timing and short in duration to be essentially ignored in the overall distribution of feeding records. The longer activity period of Group V more than compensated for the proportionately fewer feeding records each hour compared to Group P (Figure 6.2).

Seasonal variation in the temporal distribution of feeding (Figure 6.2) indicates, for Group P, earlier morning peaks in the summer Circuits III, IV & V (0900-1000) than in the winter Circuits VI, VII & VIII (1100-1300). Intense feeding bouts early in the day on the fruits of Ravensara sp. and Cryptocarya sp. during Circuit IV accounted for this peak at one time. In Group V the variable daily distribution of suckling times adversely affected smooth daily distributions of feeding records for each Circuit. In mid-summer (Circuit III), for example, an early and late feeding peak is present - a condition typical of diurnal tropical animals, and, indeed, lemurs in other regions (Sussman 1972, Richard 1973). Here, however, this bimodal distribution is associated with the fact that 65.5% of the time which the infant

Figure 6.2 Seasonal variation in the hourly distribution of feeding records for each study group at Analamazoatra.

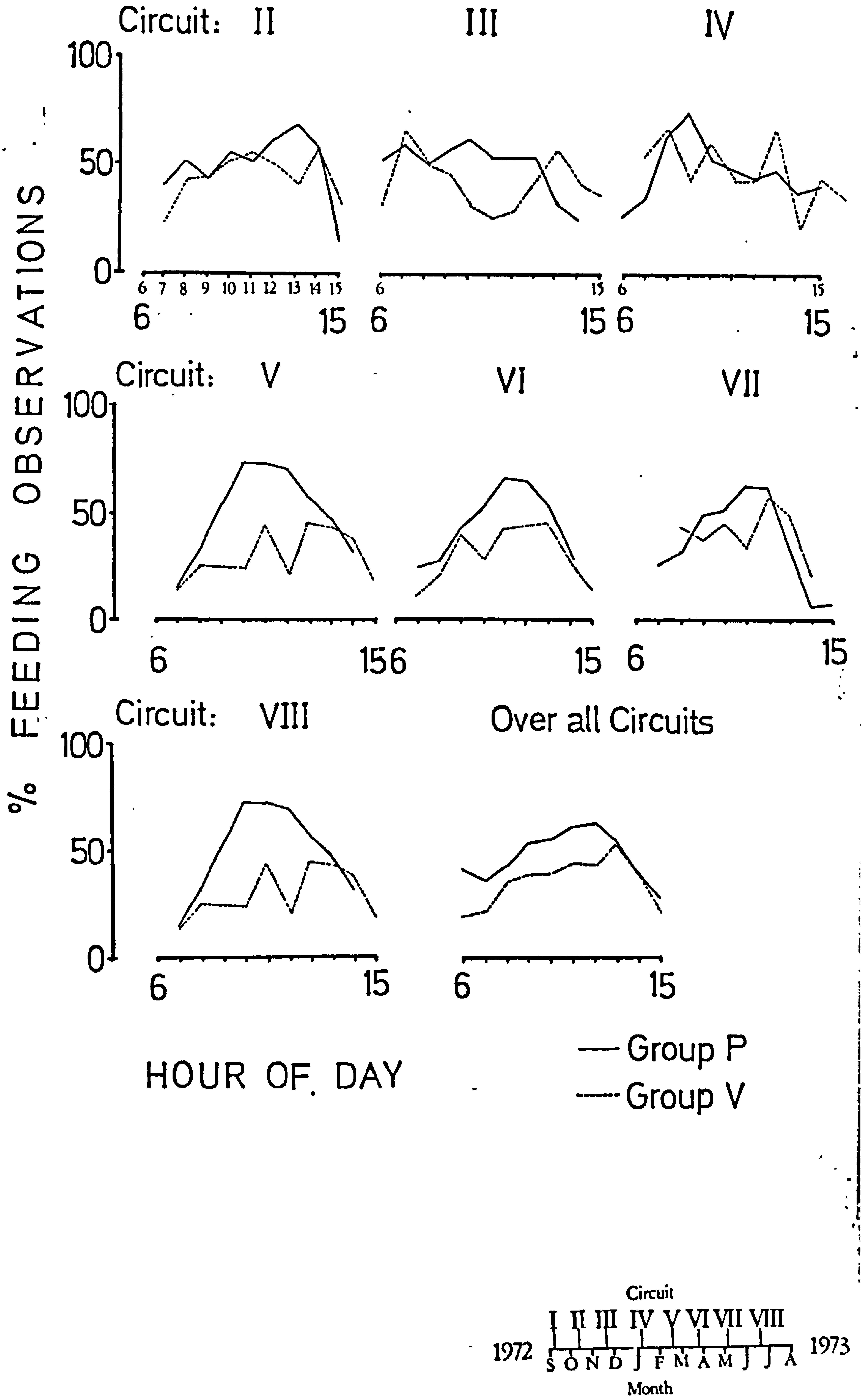

Circuit: II
III
IV
100
50
0
6 7 8 9 10 11 12 13 14 15
6
15
Circuit: V
VI
VII
Circuit: VIII
Over all Circuits
% FEEDING OBSERVATIONS
HOUR OF DAY
Group P
Group V
Circuit
I II III IV V VI VII VIII
1972
1973
S O N D J F M A M J J A
Month

Fig 5

suckled the mother occurred between 10.00 hours and 12.00 hours at this time of the year. Towards the end of the study as the infant was weaned the daily distribution of feeding activities (and the duration of the activity period itself) more closely approached that of Group P.

Temporal distributions of feeding showed no marked differences between individuals (Figures 6.3a, 6.3b).

2.4. The amount of time spent on different foods.

2.4.1. Food species.

At least 62 species of plant were seen to be eaten by *Indri*[1]. All 62 species could be ascribed to a genus, but only 24 (39%) were specifically named. Feeding observations in both groups suffered 10.8% records where the food being eaten could not be determined. This was either because the food could not be properly seen or because it was an unknown food. Identified food species, using the classification of Hutchinson (1973), are located in 19 families including:

> Clusiaceae (7 species), Annonaceae (4 sp.), Lauraceae (3 sp.), Euphorbiaceae (3 sp.), Sapindaceae (3 sp.), and eleven families each represented by a single species.

A maximum of 16 species consumed by Group P were not observed to be eaten by Group V and 5 species consumed by Group V were not observed to be eaten by Group P. This

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[1] See Appendix 4 for a list of food species.

Figure 6.3a The hourly distribution of feeding by each individual in the 2 study groups at Analamazoatra over the whole year.

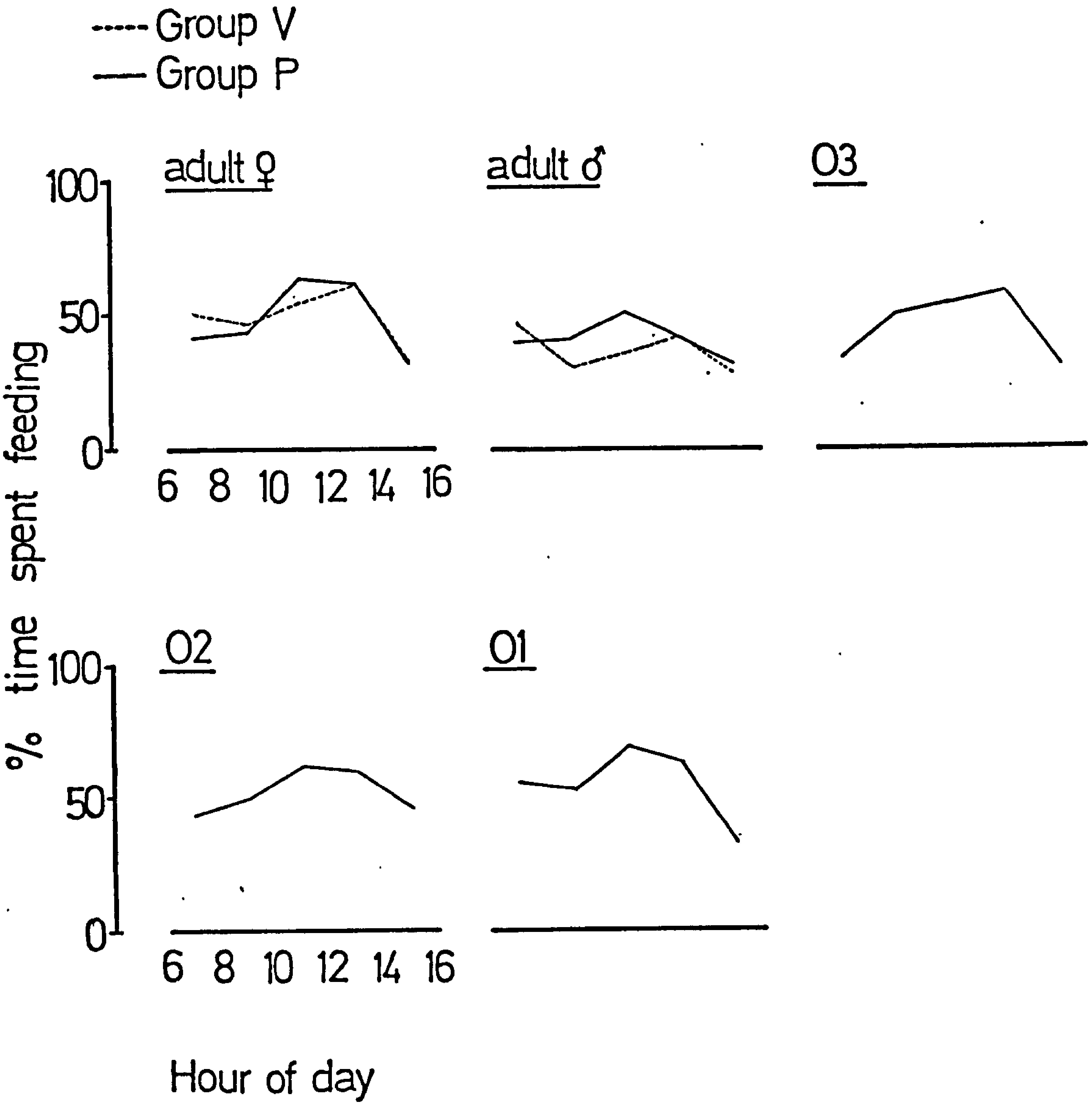
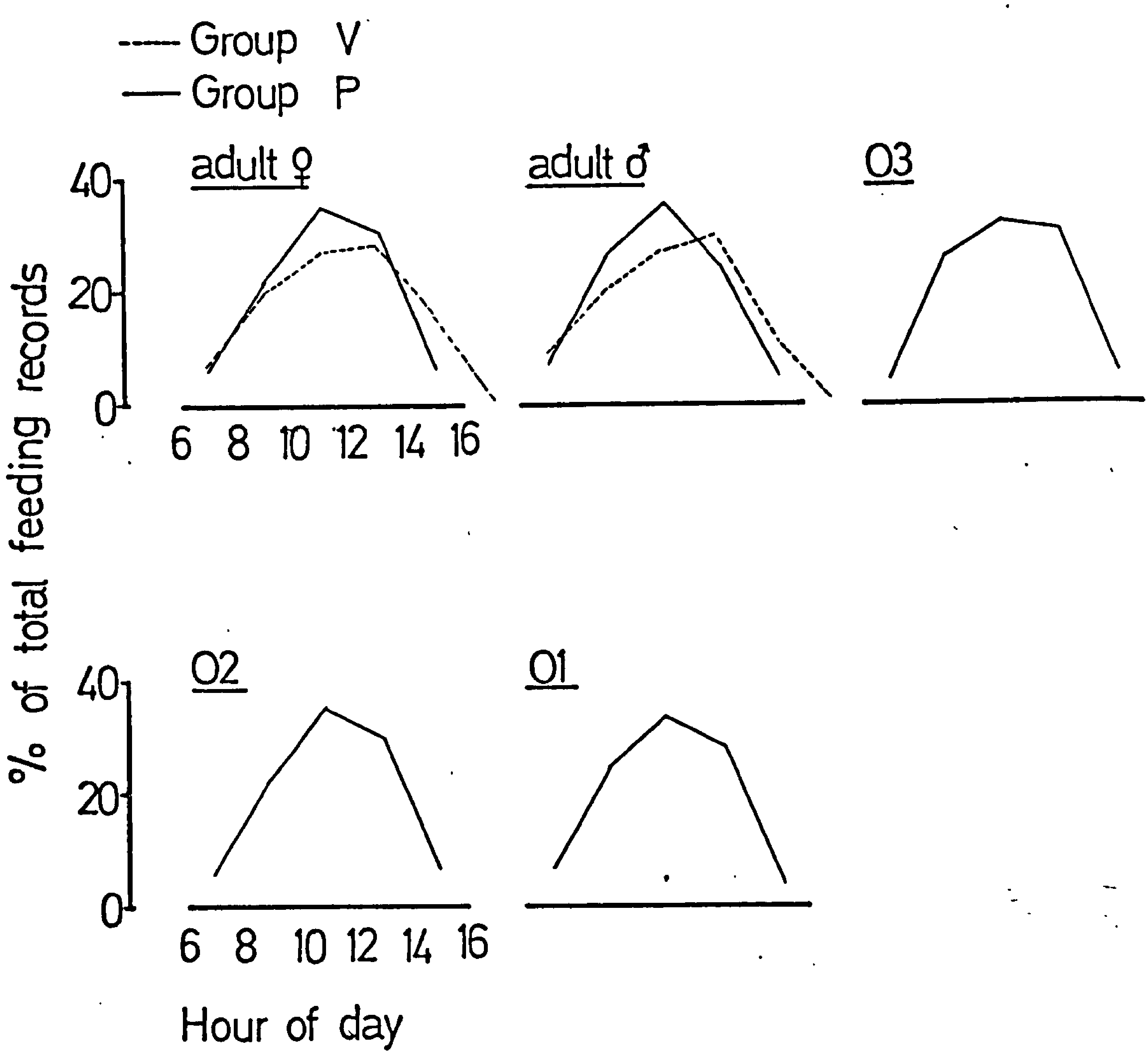

Group V
Group P
adult ♀
adult ♂
O3
O2
O1
100
50
0
6
8
10
12
14
16
% time spent feeding
Hour of day

Figure 6.3b The proportion of all feeding records, by each individual in the 2 study groups at Analamazoatra, that occur in each hour of the day.



Group V
Group P
adult ♀
adult ♂
O3
O2
O1
% of total feeding records
40
20
0
6
8
10
12
14
16
Hour of day

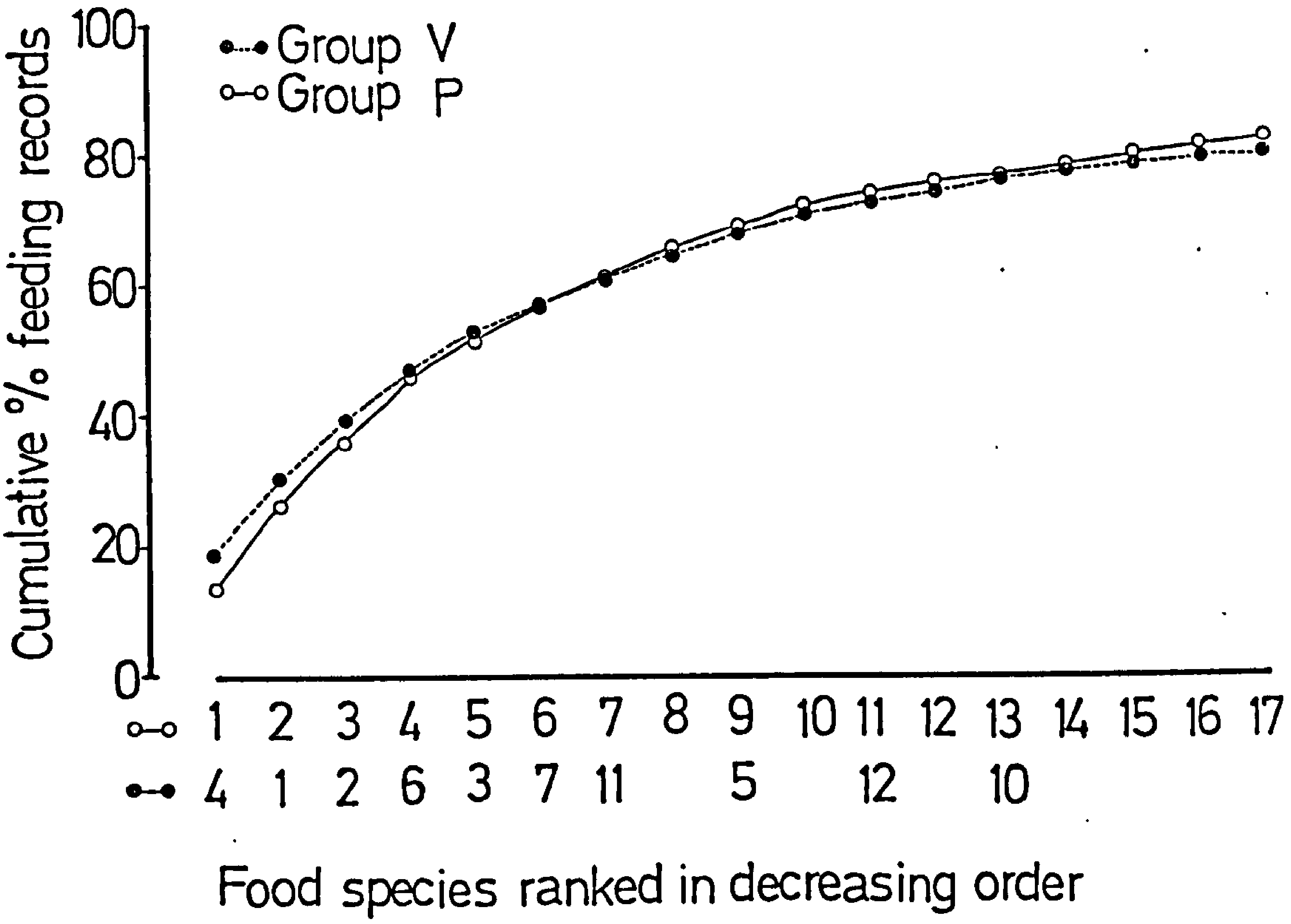
was most likely due to differences in the period of observation in each Circuit and not to inter-group variation in selectivity or availability. Of the 21 species consumed by one group but not consumed by the neighbouring group, 14 (66.7%) were eaten only once during a single Circuit, and the remaining 7 totalled only 1.1% of the feeding records of Group V and 3.3% of the feeding records of Group P.

In practice, foods eaten on more than one occasion were later identified and it is therefore unlikely that the species' complement of each group's diet differed considerably.

As well as essential identity in the 2 groups' choice of species, each group tended to concentrate more on some species than others (Figure 6.4). Group P spent 13.9% of its feeding time on the top ranking species and 50% on the top ranking 5 species. Group V spent 19.0% of its feeding time on the top ranking species and 50% on the top ranking 5 species. Four of the top ranking 5 species and 10 of the top ranking 13 species were common to both groups.

Differences in diet between the two groups appeared to be related more to the amount of time each group spent on each species than to the choice of species itself, as 83.3% of the species eaten by Group V were also part of the diet of Group P. Whether variation in the amount of time spent on specific food species was due to local variation in availability, different needs or personal

Figure 6.4 Food species selection. The cumulative percentage of time spent by each study group on those food species comprising at least 1.5 % of the feeding records. Ranking of food species is made for Group P and these rank numbers are retained for food species ranking of Group V.


Group V
Group P
Cumulative % feeding records
100
80
60
40
20
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
4 1 2 6 3 7 11 5 12 10
Food species ranked in decreasing order

preferences could not be examined as no measures of food abundance were recorded. Clumps of food of one species were in at least some cases largely responsible for concentrated feeding by one group and not the other (see Section 7).

Group IV at Vohidrazana was observed feeding on at least 10 identified plant species, only one of which had not been consumed by Indri at Analamazoatra.

2.4.2. Food parts.

The two study groups did not differ extensively in the amounts of time they fed on various food items (Table 6.1). Seasonal variation in food part consumption was clearly associated in most cases with changes in availability resulting from phenological cycling of the vegetation. Peaks in the seasonal distribution of consumption of each food part in each group (Figure 6.5) could be generally attributed to concentrated feeding on a single species or even a few trees of one species. The great increase in fruit eating during the middle of the study period, for example, was clearly invoked by the synchronized fruiting of a few, large Cryptocarya olseodaphnifolia in the home range of each study group at Analamazoatra. Similarly, the small overall amount of time spent feeding on flowers was due only to a single species of Symphonia in Circuit III and Ocotea in Circuit V.

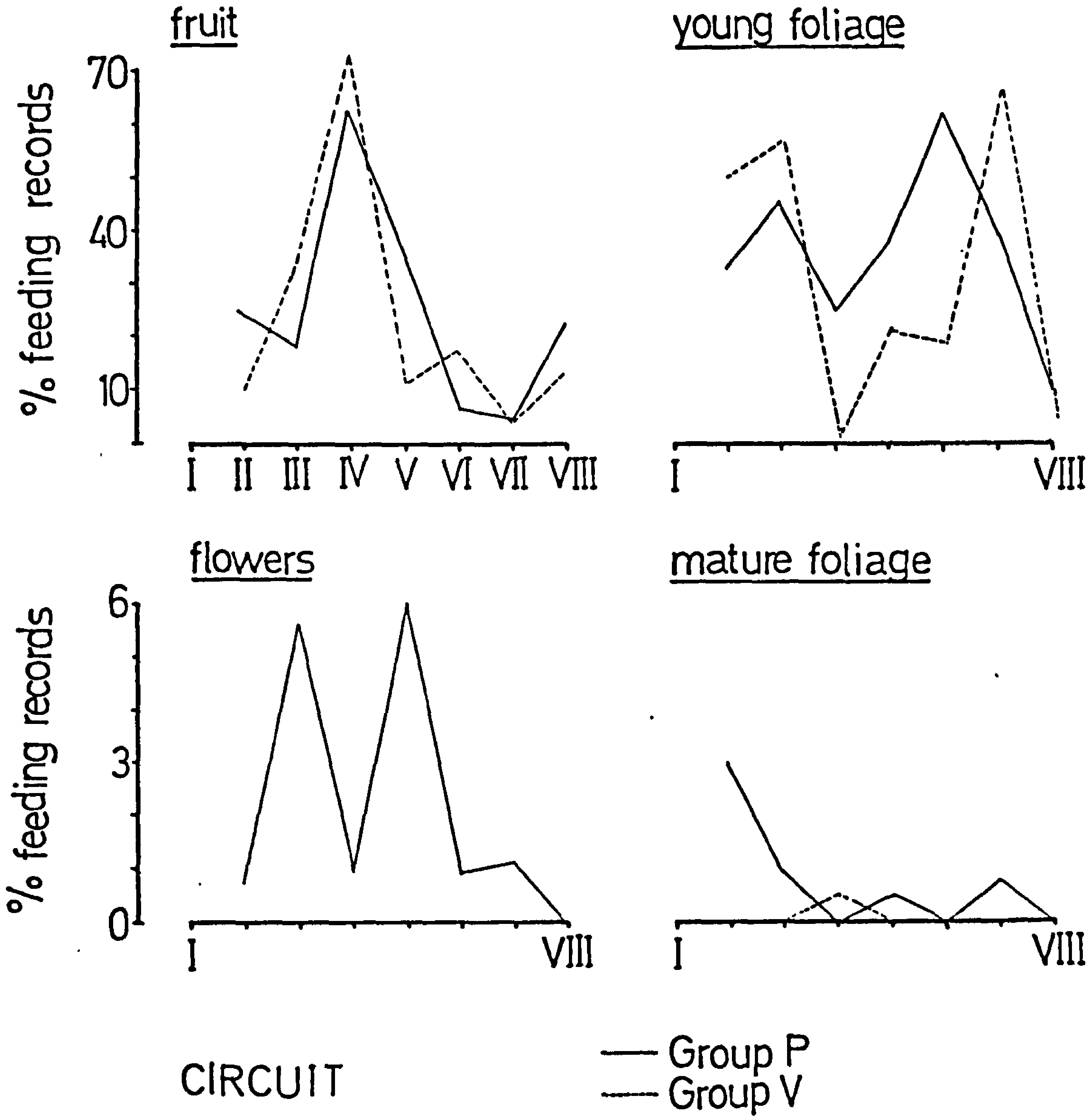
Young foliage, ranging from leaf shoots to large, flexible but clearly immature leaves, provided the main parts of both groups' diets. Group IV at Vohidrazana

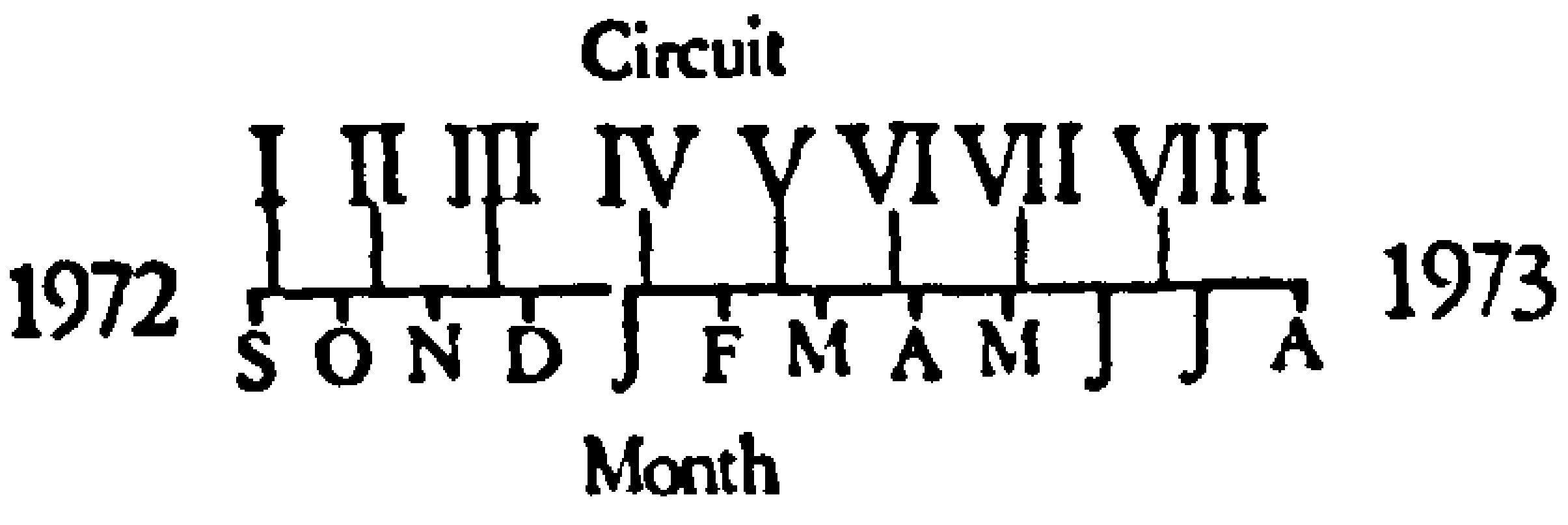
	Leaf buds, shoots of young leaves	FRUIT	FLOWERS	MATURE LEAVES	?
GROUP P	36.1	26.4	2.3	0.9	14.3
GROUP V	32.2	23.8	0.0	0.2	43.8

? = unidentified part (probably mostly young foliage).

TABLE 6.1. Differences in food part consumption between groups (% feeding observations).

Figure 6.5 Seasonal variation in food part consumption for Group P and Group V.


fruit
young foliage
flowers
mature foliage
% feeding records
70
40
10
% feeding records
6
3
0
I
II
III
IV
V
VI
VII
VIII
I
VIII
I
VIII
I
VIII
CIRCUIT
Group P
Group V


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
1973
Month

also ate predominantly young leaves. Fruit when available were, however, preferred and consumed earlier each day and for longer periods. Other items, such as mature leaves, were fed on regularly but in small amounts. Feeding on the adult foliage of Dilobeia thouarsii, for example, was confined both for Group P and Group IV to one, complete leaf per individual every few days.

The sampling technique employed did not permit statistical comparisons of food type consumption between groups to be made, but differences were not obviously marked. Group V, however, were never seen to eat flowers.

On about 75% of the observation days each Indri group consumed very small quantities of earth exposed by upturned tree trunks. All group members sequentially and momentarily fed on the earth in a specific spot that would be returned to some days later (Plate 6.4). There appeared to be from 5-10 such earth feeding sites in each territory. An analysis of one soil sample (Table 6.2) failed to show high concentrations of specific minerals. Earth feeding by folivorous primates has been observed in Colobus guereza (Oates 1975), Gorilla gorilla berengei (Goodall, pers. comm.), Pan troglodytes troglodytes and Hylobates (Hladik and Guegen 1974), and in many human populations. To date there is no evidence that specific minerals are obtained by this behaviour in concentrations exceeding that of the vegetation they eat (Hladik & Guegen 1974, Oates 1975).

PLATE 6.4 Juvenile *Indri* (Group V) feeding on earth from an upturned tree-trunk.

N	P	Ca	Mn	K	Na	
0.18	0.026	0.014	0.0036	0.0071	0.0057	(i)
0.15	0.024	0.014	0.0036	0.0071	0.0057	(ii)

TABLE 6.2. Soil feeding.
(% dry weight mineral content in consumed soil)
two samples tested.

---

n Circuit:	II	III	IV	V	VI	VII	VIII
8-10	3	3	2	2	3	2	3
5-8	4	4	5	3	2	4	4
3-4	3	4	3	5	2	4	2
<2	9	13	11	11	11	9	12

TABLE 6.3. The number of days (n) each Circuit that different numbers of species were eaten by Group P.

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3. SELECTIVITY

3.1. Species selectivity.

No botanical censuses of forests inhabited by Indri were performed, but it was nevertheless clear that most Indri foods at Analamazoatra were produced by the commonest trees of the forest. A 0.73% plant census was carried out by a government department in 1970 in one of the study areas (Fierenana), a region similar to Analamazoatra in botanical constitution. Referring the results of this census to information obtained in the present study, it was found that of the 20 commonest plant species, 12 were much eaten food species accounting for 82.6% (Group P) and 75.1% (Group V) of the feeding records. These 12 species accounted for 58.7% of trees with breast level diameters of at least 30 cms., but only 8.9% of the forest's total identified species complement.

3.2. Intra-specific selectivity.

Despite feeding most apparently on widely available foods, Indri in Group P sometimes exhibited great selectivity within species. This was particularly noticeable when animals were observed to consistently select as food only one of a pair of adjacent or nearby trees, although both were in an appropriate and identical phenological condition. The unripe fruit of Cryptocarya olseodaphnifolia, for example, were consumed daily during Circuit IV from 3 trees situated on the western edge of Group P's home range and one large tree in the south-western corner (see Section 7). In Circuit VII, after fruiting, all these trees flushed synchronously into new leaf, but the group of Indri fed only in the solitary tree, despite visits to both locations and complete consumption of that tree's young leaves. In Circuit VIII the fruit of Ocotea sp. were consistently and repeatedly eaten by Group P from only one of two neighbouring trees so close together that their trunks touched each other.

The function of this form of intra-specific selectivity, which was not observed in Group V, is uncertain. Group P may have been exercising some strategy of cropping by acting in this way, thus diminishing the harmful effects of repeated visits and ensuring an adequate supply of food for the future. Primates have been shown to affect the structure of trees (Oppenheimer & Lang 1969), but the consequences in terms of future productivity are less clear. An alternative, and probably more likely interpretation, is that slight taste preferences common to all members of the group were manifested in this way. The animals may have been averse to some individual trees because they contained high concentrations of toxic substances. Why, however, this should be the case in one group and not the other is unclear. The observation may be tentatively cited as circumstantial evidence for a satisfactory, if not abundant supply of food for Group P at some times of the year.

4. DIETETIC DIVERSITY

During any 10-day Circuit between 19 and 27 (mean 21.7) species were consumed by Group P and during any 6-day Circuit between 13 and 24 species (mean 18.7) were consumed by Group V. The mean number of different[1] species that were consumed by each group in every 6-day observation period were identical at 17.5 (Figure 6.6).

In any one day, however, between 5 and 11 species were chosen. These usually included a concentrated food source that was temporarily available e.g. one or two large fruiting trees, several species that carried new leaves, and one or more species that were consumed throughout the year. The concentrated food source would be consumed daily, whereas the inclusion of other food types in the diet could change between days. I gained the distinct impression that this day to day variability was, in some cases, rigorously applied as some species, within that Circuit's repertoire of foods, despite being repeatedly approached were consumed on some days but not on others.

The distribution of the number of species eaten daily (Figure 6.7) shows a mean minimum number of species (where all undetermined foods were assumed to be <u>similar</u> to those otherwise eaten that day) for Groups P and V of 7.7 and 7.6 respectively. The related mean <u>maximum</u> number of species (where all unidentified foods are assumed to be <u>different</u> from those otherwise eaten) for Groups P and V was 9.0 and 10.0 respectively. The daily distributions

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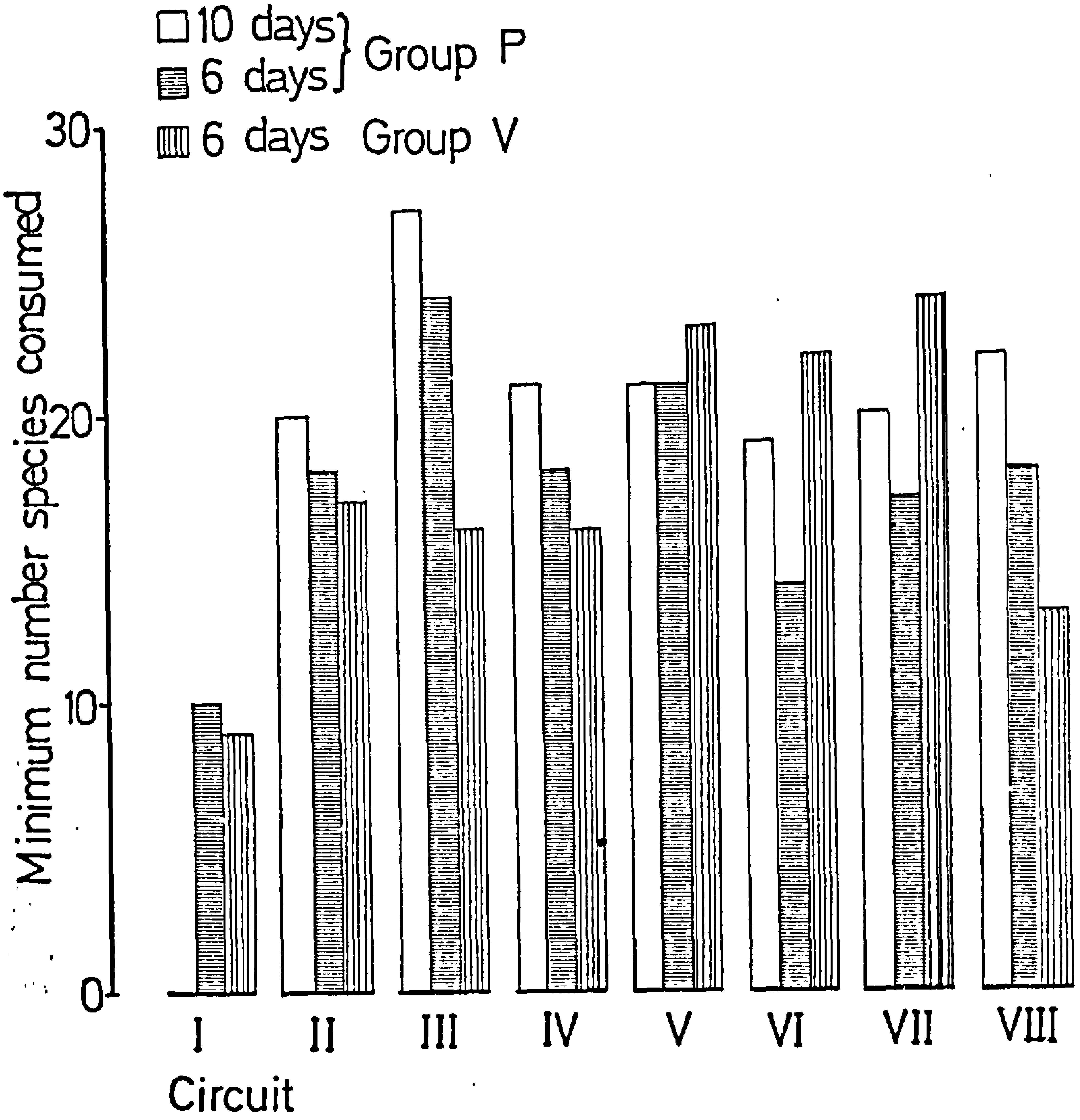
[1] excluded from this calculation are unidentified species.

Figure 6.6 Minimum numbers of species of food consumed by each study group at Analamazoatra during each Circuit. Group P data are presented for 6 days' observations as well as 10 days' observations, for comparison with Group V.


□ 10 days
▤ 6 days
Group P
▥ 6 days Group V
Minimum number species consumed
30
20
10
0
I
II
III
IV
V
VI
VII
VIII
Circuit

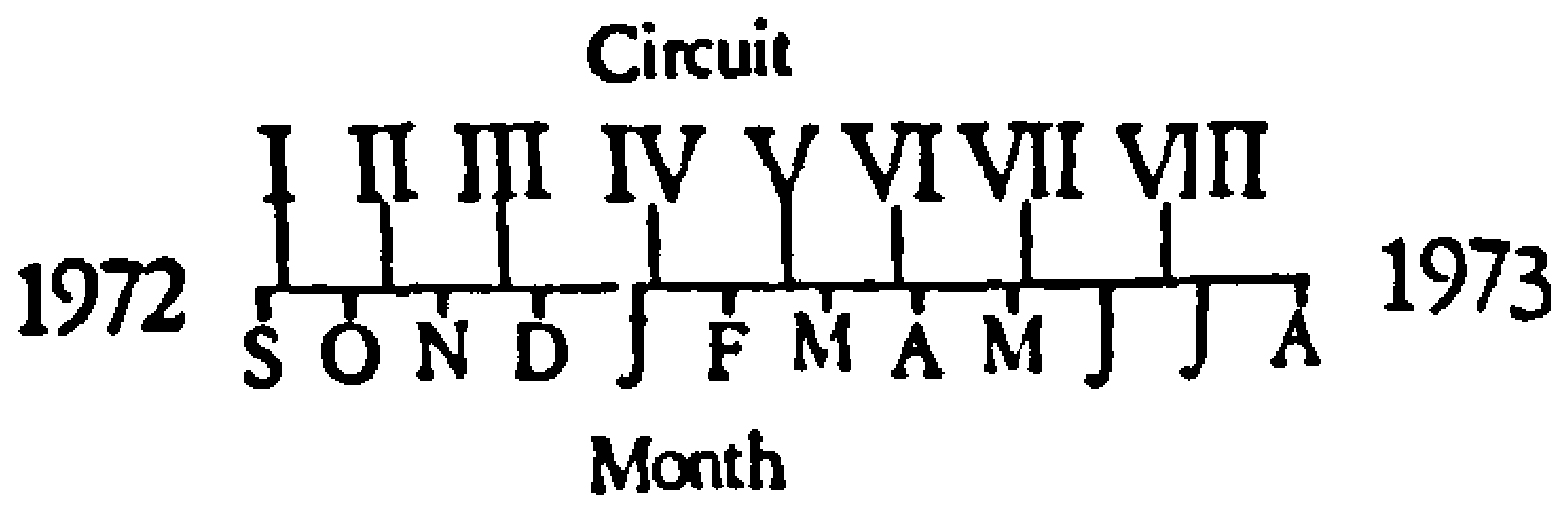
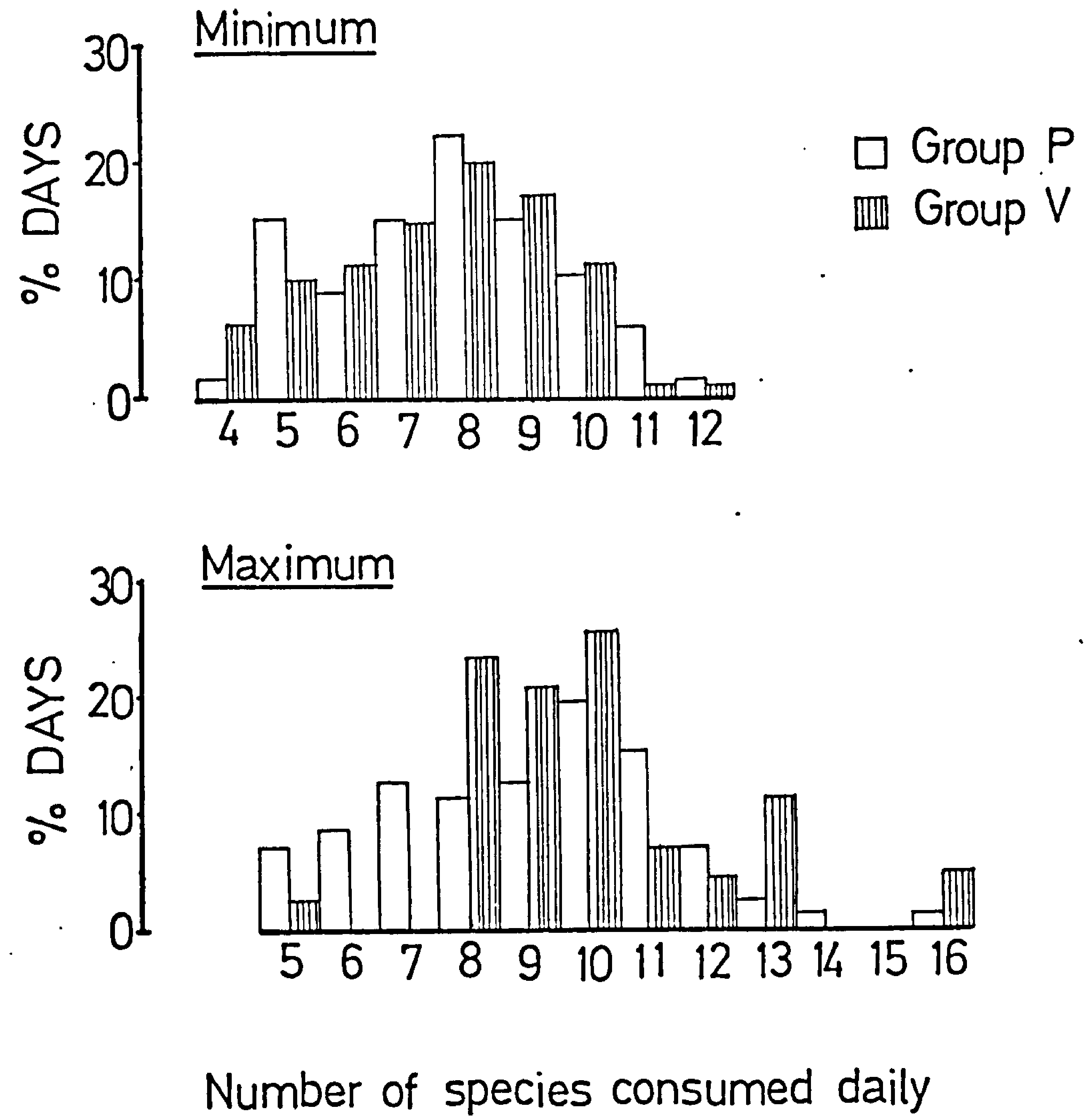

Circuit
I II III IV V VI VII VIII
1972
S O N D J F M A M J J A
1973
Month

Figure 6.7 The number of species consumed daily by Group P and Group V.

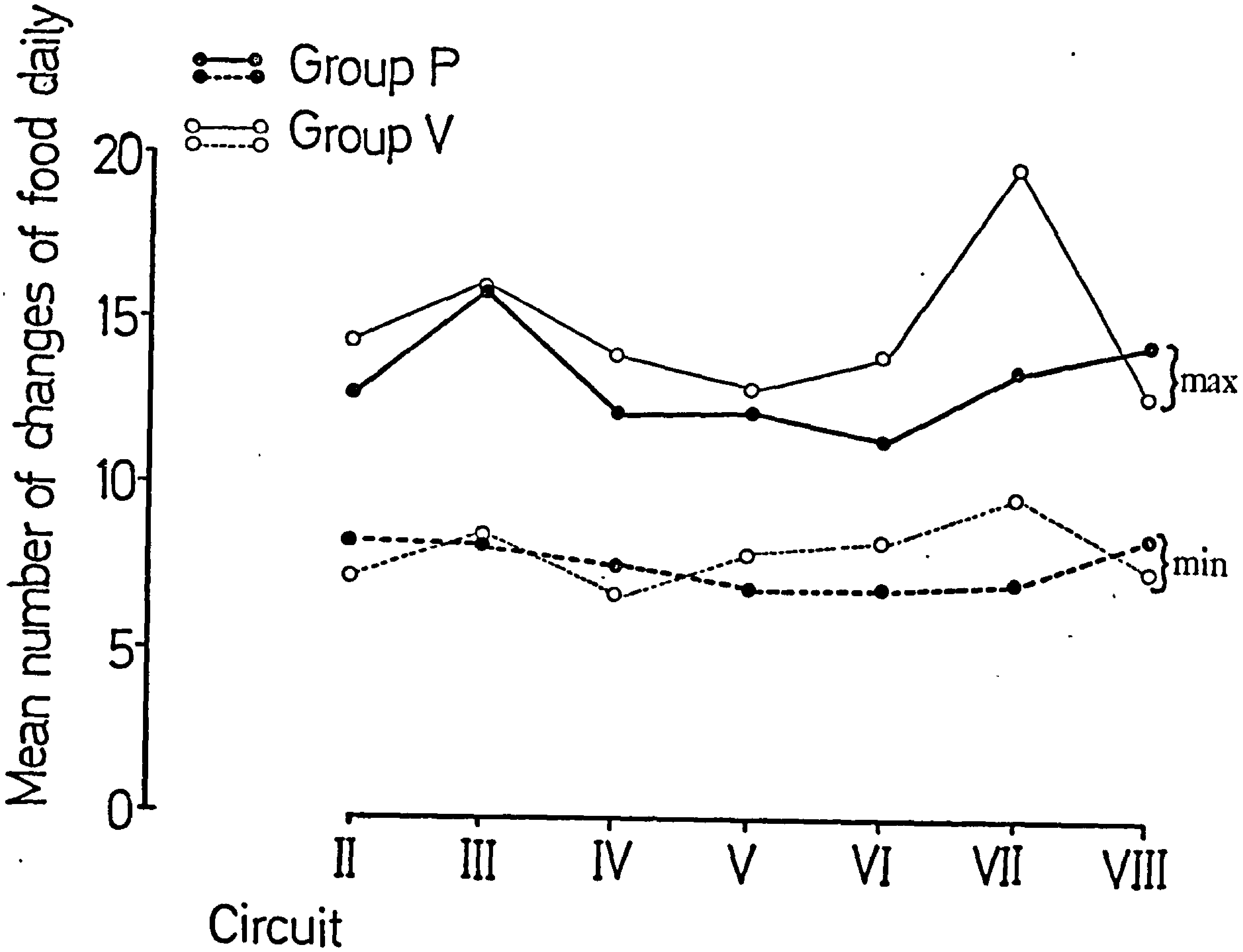
The minimum number of species consumed daily is that number of species where all unidentified records consisted of foods assumed to have been already eaten that day. The maximum number of species consumed daily is that number of species where all unidentified records consisted of foods assumed not to have been already eaten that day.

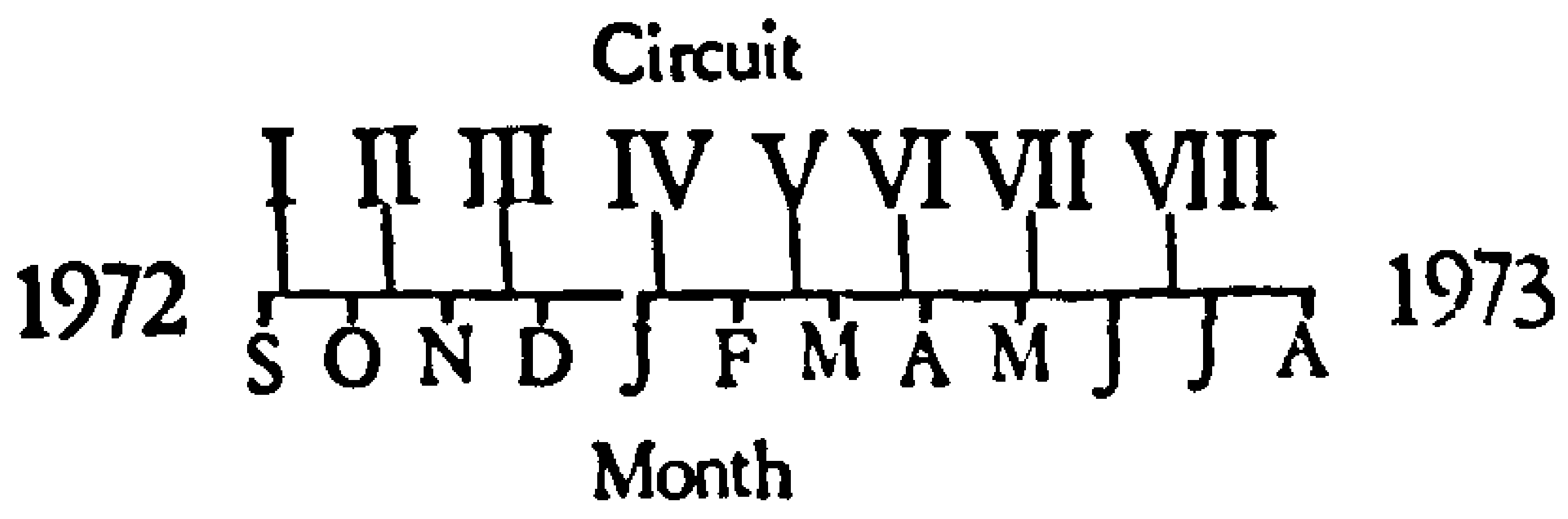

Minimum
30
20
10
0
% DAYS
4
5
6
7
8
9
10
11
12
□ Group P
▥ Group V
Maximum
30
20
10
0
% DAYS
5
6
7
8
9
10
11
12
13
14
15
16
Number of species consumed daily

of the numbers of species eaten did not differ greatly between the two groups, but it is possible (due to the method by which the data was analysed) that Group V members selected for more dietetic variety than those in Group P. This is because the members of the latter group were sometimes feeding on different species at the same time and therefore the number of species eaten by each individual was occasionally overestimated. In addition, feeding bouts were shorter and the frequencies with which animals changed trees were greater in Group V (see Chapter 7).

The rate at which each group switched to feed on a new species did not differ between the two groups (Figure 6.8). The slightly higher maximum figures for Group V were probably more a consequence of poorer food species identification than inter-group variation. The rate at which the groups changed foods and the daily numbers of species eaten are seen to be constant over the year. Furthermore, the mean values for the numbers of times each group changed foods closely approximated the numbers of species eaten each day. Most species, therefore, were eaten on average at only one time each day, although several different trees of one species may have been successively entered. This conferred an impression of a highly organised system of feeding and ranging behaviour on the observer (see Section 5) with one notable exception: a single species, Ravensara pervillei, whose fruit and foliage provided for both groups the most consistent source of nutrition throughout the study period, was eaten

Figure 6.8 The rate at which food species were changed in each group. For each study group at Analamazoatra seasonal variation in the mean maximum and mean minimum number of food changes made each day are illustrated. The maximum figures consider all unidentified food species to be different from those previously chosen. The minimum figures consider all unidentified food species to be the same as those previously chosen.


Group P
Group V
Mean number of changes of food daily
20
15
10
5
0
max
min
II
III
IV
V
VI
VII
VIII
Circuit


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
1973
Month

apparently wherever the animals approached it. It is probably no coincidence that individual trees of this species were obviously phenologically asynchronized, each tree retaining fruit and young leaves for long periods of time.

5. TEMPORAL PATTERNING OF FOOD CHOICE

Indri at Analamazoatra selected for variety in addition to bulk consumption. Those foods consumed virtually every day were also those foods of which most feeding records were comprised, whilst relatively large numbers of species (about 50%) were eaten once or twice during the short observation periods every 6 weeks (Table 6.3).

5.1. Feeding continuity.

5.1.1. Methods.

Two approaches to the presentation of food choice stochastics may be entertained. These may, if animals convert to new foods with sufficient frequency, provide quantitative evidence for some temporal organisation of species choice.

(i) Sequences of food species' consumption may be considered as single or multiple chain Markov processes (or mixtures of these) and the observed changes of food compared with transitions expected by random association. For example, the selection of food may be dependent solely on that immediately previously chosen and approximate, therefore, to a second order process only.

This approach was profitably utilised in Altmann's (1965) study of the stochastics of behaviour in *Macaca mulatta*.

In a sample of data the expected number of times (E) a specific event (k) follows another specific event (j) is given by:

$$E(j,k) = N_2 \bar{p}\ (j,k) \qquad \ldots\ldots \quad (1)$$

where N_2 is the total number of observed behavioural transitions, $\bar{p}$ the observed probability of an event occurring n times out of N_1 observations. It should be noted that transitions between point-sampled behavioural records are not strictly behavioural transitions. Where bout lengths of the behaviours are greatly in excess of the inter-point sample interval, however, they constitute a reasonably accurate approximation.

As the probability of the occurrence of two 'independent' events is equal to the product of the probabilities of each event:

$$\begin{aligned} E(j,k) &= N_2\ \bar{p}(j)\ \bar{p}(k) \\ &= \frac{\left\{N_2\ n\ (j).\ n\ (k)\right\}}{N_1^2} \qquad \ldots\ldots \quad (2) \end{aligned}$$

Where sequences of identical behaviour are sought ($\bar{p}$ (j,j)) represented here as $\bar{p}$ (j^o,j^1), (2) above must be slightly modified as the first time j occurs alters the probability that it will occur again.

$$E(j^o, j^1) = N_2\, \bar{p}\,(j^o) . \bar{p}\,(j^1)$$

$$= \frac{N_2\{n(j) . (n-1)(j)\}}{N_1^2}$$

$$= \frac{N_2}{N_1^2}\left\{n(j)^2 - n(j)\right\}$$

$$= \frac{N_2\, n(j)}{N_1^2}\left\{ n(j) - 1 \right\} \qquad \ldots\ldots (3)$$

If N_1 is small this expression should be multiplied by Bessel's correction, $\frac{N_1}{(N_1-1)}$.

As the degree of difference between the expected and observed frequencies of transitions cannot be predicted it is impossible to know what value of n(j) would permit this difference to be statistically tested. It is difficult to decide, therefore, for how long a group should be watched in order to verify such a difference.

(ii) Examination of inter-choice intervals[1] may expose overall clusterings of food types over time. This possesses the 'advantage' that unlike (i) above these clusterings are unrestricted to specific order approximations.

5.1.2. Results.

Only individuals for whom the most complete data were obtained (i.e. individuals top in the hierarchy each day) provided information for the analysis of feeding continuity. It is felt that as food choice apparently

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[1] Inter-choice intervals are the number of different species eaten between successive observations of feeding on the subject species.

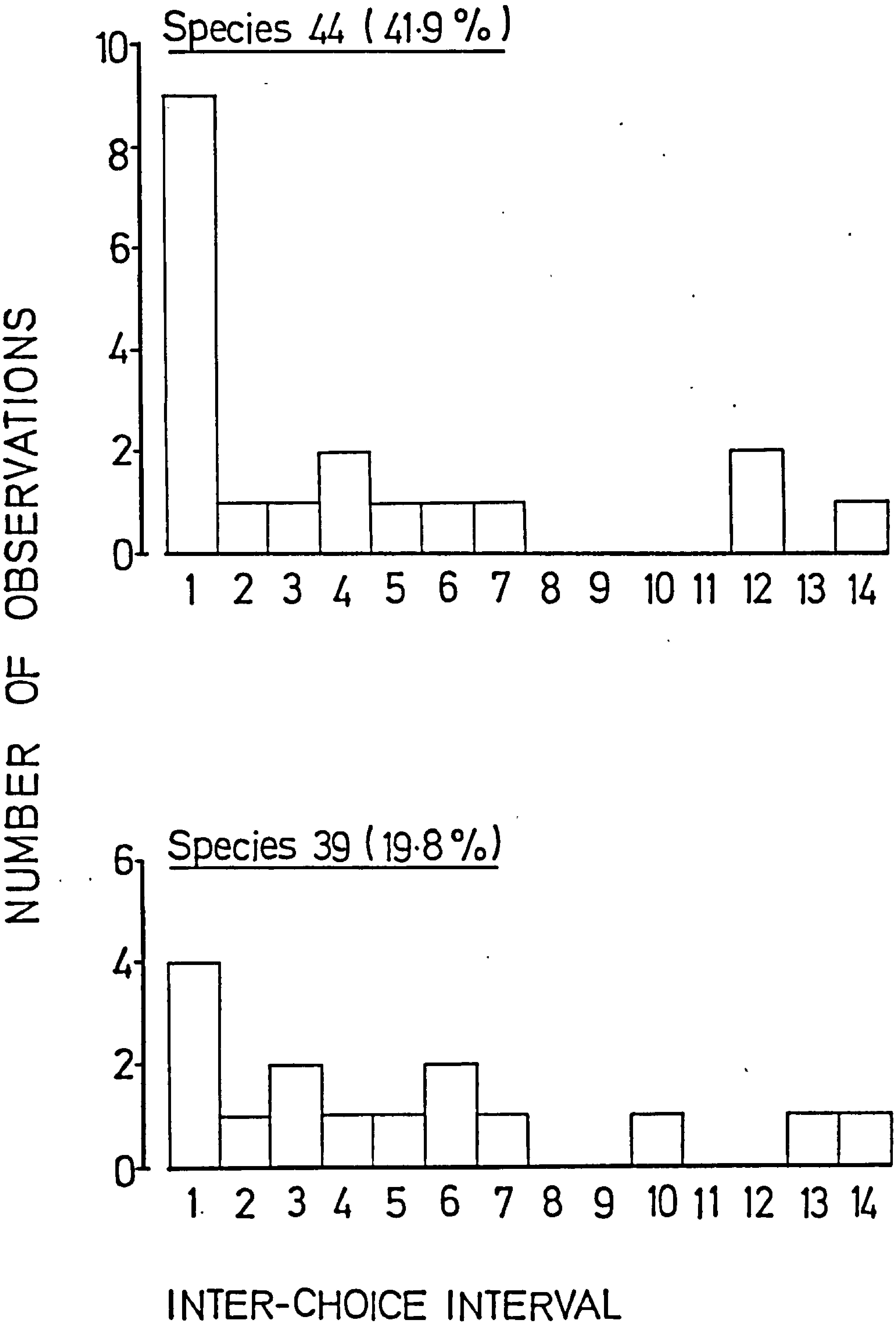
varied little between individuals, their data can be justifiably considered as representative of the behaviour of the whole group.

(i) Method 1: A heavily fed species, No.44, was consumed in Group P by followed individuals on 19 occasions during Circuit VIII. The total number of feeding bouts (where a different tree was fed upon) recorded during this Circuit was 87, species 44 accounting for 41.9% of feeding observations. The observed number of times animals changed trees yet continued feeding on species 44 was 8, whereas the expected frequency from equation (3) above was 4.38. Although this result is suggestive of a tendency for Group P to continue feeding on the same species at another location, the small numbers prohibit statistical confirmation.

(ii) Method 2: Considering the complete observation period of Circuit VII as comprising 87 successive feeding bouts, the distribution of inter choice intervals of the same species (No.44) may be constructed (Fig.6.9). Despite suggestive distributions, the period of observations is again seen to be too short to confirm same-species feeding dependency.

For Group V the even shorter Circuits prohibited comparative quantitative attempts to measure continuity in food species consumption. Species numbers 44 and 61 appeared to be those most often eaten again in a different tree (i.e. 'continued') and these two species probably comprised the most clumped distributions of food in their territory, and were major food items.

Figure 6.9 Feeding continuity in Group P. For 2 top-ranking food species during Circuit IV the number of choices of foods between successive choices of the subject species (inter-choice interval) are illustrated. The % of feeding observations on the two species are also shown.


Species 44 (41·9 %)
10
8
6
4
2
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Species 39 (19·8 %)
6
4
2
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14
NUMBER OF OBSERVATIONS
INTER-CHOICE INTERVAL

Instances of minor feeding continuity took 2 forms:

(i) when a little eaten species was repeatedly consumed during a single day at different sources, and;

(ii) when a little eaten species was immediately consumed again at a different source.

Species fed on for small overall amounts of time were generally widely scattered about the forest and geographical proximity could not have accounted for observations of feeding continuity involving them. On the 3rd day of observations on Group P during Circuit IV, for example, species 33 was eaten on 4 separate occasions. On the second day spent watching Group P during Circuit VII species 62 was also eaten in 4 separate bouts. Neither species was consumed at any other time during the respective Circuits. This type of diurnal selectivity of a species applied sometimes to food _part_ ... "....O2 feeds towards the end of the day on Varongy (_Ocotea_ sp.) adult leaves. The tree contains fruit but he doesn't touch it. None of the group have eaten Varongy fruit today ....". The observation is noteworthy for three reasons:

(i) For every other day in that Circuit, the fruit of this species was a major food item (12.5% feeding observations).

(ii) The animals had ample opportunity to eat the fruit from several trees that day because they had visited the trees anyway.

(iii) All group members fed that same day on the _adult_ leaves of the same species - an item otherwise never consumed.

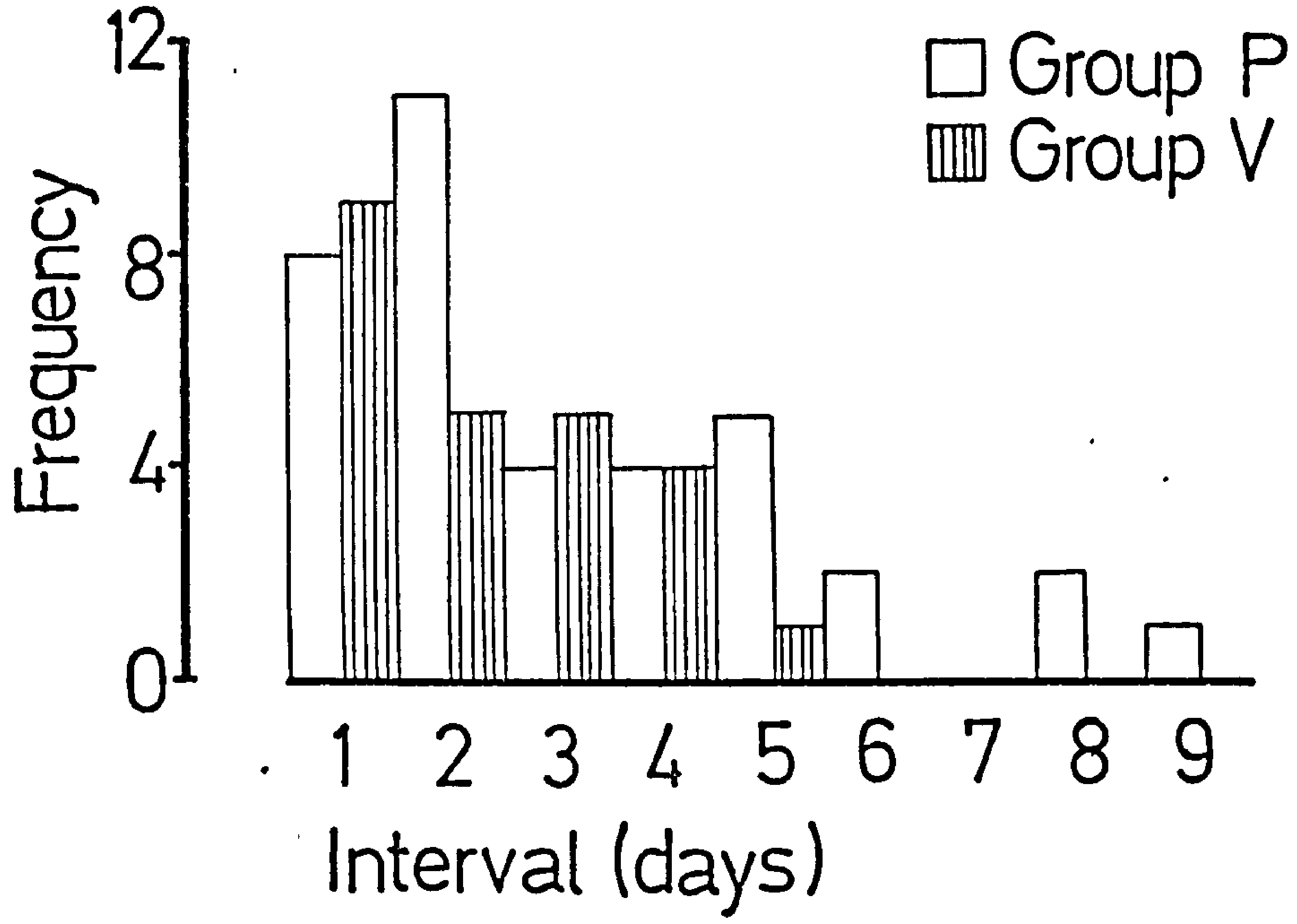
Feeding continuity was further investigated in the day-to-day clumping of infrequently fed species. In species eaten on 2 occasions only during the 10-day Circuit the number of days separating successive observations of it being eaten were compared to those expected by chance (Figure 6.10). A test was tried to compare the relative frequencies of inter-choice intervals of less than 5 days with those of more than 5 days, but this proved non-significant ($X^2_{1df} = 1.343$, $0.2<p<0.3$).

It appears therefore that feeding continuity may have been present for (i) major foods and (ii) some foods rarely eaten, but that for a large proportion of the foods it can not be supposed.

5.2. Temporal aspects of food choice.

There was no obvious temporal division of food types within each day. Major food items would normally be fed on for 2-3 hours each day and progression to the trees containing them would generally commence early on. Species fed on overall for a maximum of 5% of feeding observations each, were chosen as one of the first 3 species to be eaten in the day on 48.6% of the days and as one of the last 3 species to be eaten on 42.6% of the days ($X^2_{1df} = 0.5013$, $0.3<p<0.5$) in Group P. Corresponding figures for Group V were 38.1% and 44.6% ($X^2_{1df} = 0.323$, $0.5<p<0.7$).

<u>Figure 6.10</u> Feeding continuity in Group P and Group V. The number of days between observations of feeding on those species eaten only twice in each Circuit are shown for each group.



□ Group P
▥ Group V
Frequency
0
4
8
12
1
2
3
4
5
6
7
8
9
Interval (days)

Young leaves and foliage were consumed throughout the day. Fruit feeding was examined in terms of food choice within each day and compared to the total number of choices made throughout the year. No differences were found in either group.

There was no reason therefore to consider the organisation of Indri feeding behaviour to be based upon the time that certain foods were eaten during each day.

5.3. Daily variation in food choice.

Approximately 50% of the species consumed during each 10 day period of observations on Group P were eaten on only 1 or 2 occasions and these therefore, constituted the main source of dietetic variety for Indri at Analamazoatra. Variability in diet was thus assumed over a number of days rather than every day. Neither group's study period length was sufficiently great to properly examine this phenomenon or to recognise cyclical patterns of species consumption, although the behaviour of Indri is well suited to this approach if a single group were to be continuously observed.

Those fruit which were eaten most overall were consumed on every day whilst they were available. Only during Circuits VI and VII were there days when fruit were not eaten and very little fruit were consumed overall at these times.

From the amount of time spent in trees of one species where different food parts were present, it was clear that, other things being equal, Indri chose, in order of preference: fruit, leaf buds, young leaves, young adult-sized leaves, leaf stalks, leaf bases and mature leaves. A tree containing fruit, for example, would be completely stripped and although this was not an uncommon observation in the case of small trees in a flush of new leaves, there were many exceptions. On no occasion was a major food item totally consumed in one feeding bout, although saplings, which may have been relocated only with difficulty, were frequently and efficiently cropped of all the obtainable young, red foliage.

6. SEASONAL VARIATION

Very few if any food trees in either group's territory fruited or came into new leaf annually. The production of food was not measured and there are no published data available (but see Chapter 4). In any case, the 15-month research period was of too short a duration to ascertain regular or seasonal differences in the forest.

Generally, the diet of Indri gradually changed completely over a period of 2 or 3 months. Mid-summer and mid-winter foods for Group P contained 12 common species out of a total of 22, but in only one case was the same part of the same species eaten. For Group V, 11 common species were consumed out of a total of 23, and in 6 species the same part was eaten at both times of the year. Dietetic differences between successive Circuits and between seasons did not themselves differ and there is, therefore, no reason to consider parameters of nutrition in Indri in terms of slowly changing seasonal variation. For example, mid-summer (Circuit IV) stands out as the period when most time was spent on fewest species (Fig. 6.11), although the activity period was at its longest and the greatest number of feeding observations recorded. During this Circuit the top ranking species accounted for 59% and 55% of feeding observations for Groups P and V respectively. Group P retained this highly selective feeding for the following Circuit whilst Group V returned to a more evenly distributed diet. Dietary specialisation at certain times of the year is seen, therefore, to depend largely on specific, suddenly available food sources and not to arise in response to gradually changing seasonal effects.

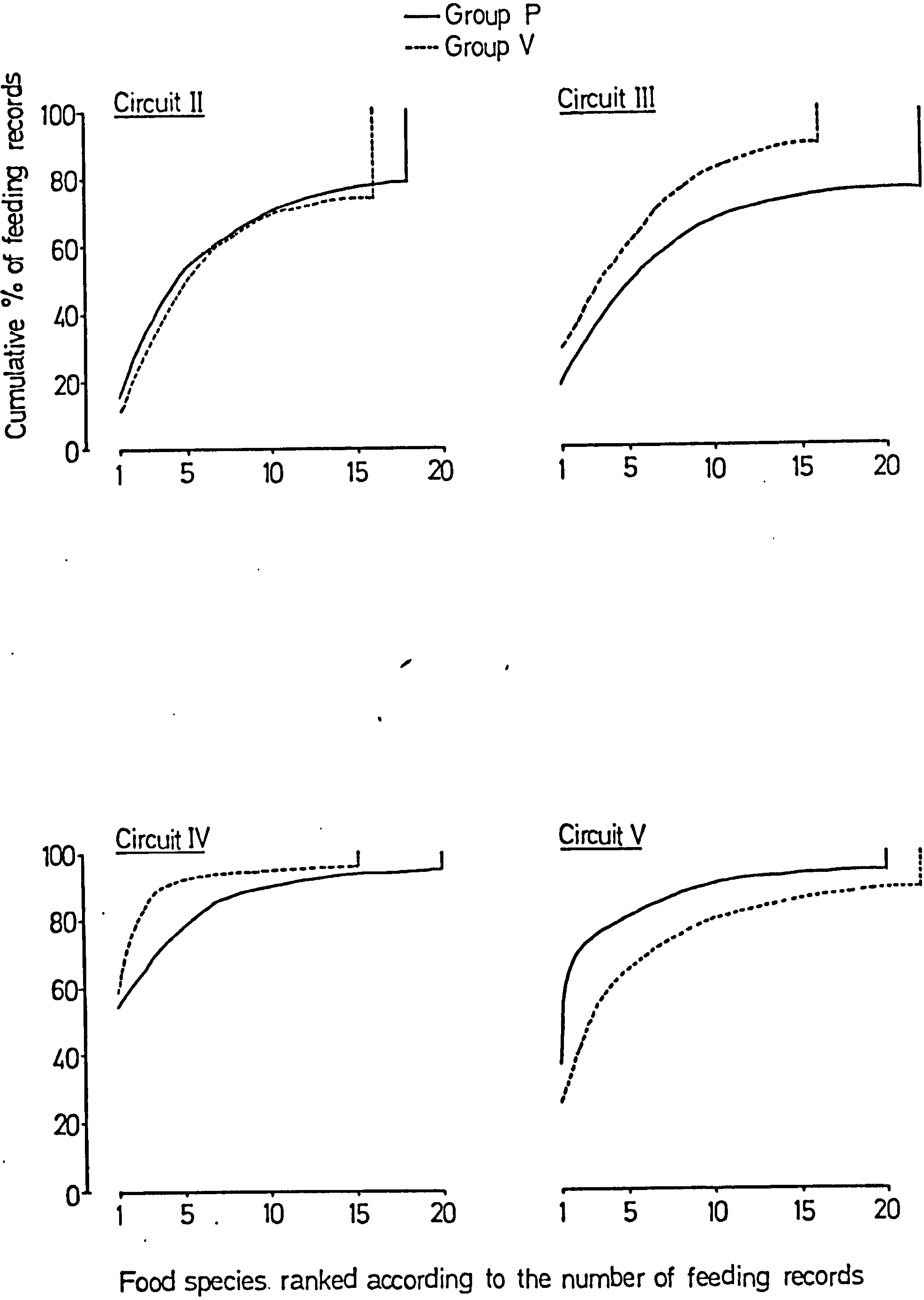
7. SPATIAL VARIATION

In order to investigate the spatial distribution of feeding sites the location of major food sources, where at least 30 minutes had been spent feeding over the year's observations, were plotted on maps of the territories of each group (Fig. 6.12).

(a) Group P

The feeding locations of 4 of the top 5 species (comprising 57.1% feeding observations) were found to be widely distributed about the ranging area. One species, however, Cryptocarya olseodaphnifolia, had a restricted distribution and was only eaten during 3 Circuits. In

Figure 6.11 Seasonal variation in the selection of species for Group P and Group V.


Group P
Group V
Circuit II
Circuit III
Circuit IV
Circuit V
Cumulative % of feeding records
0
20
40
60
80
100
1
5
10
15
20
Food species ranked according to the number of feeding records

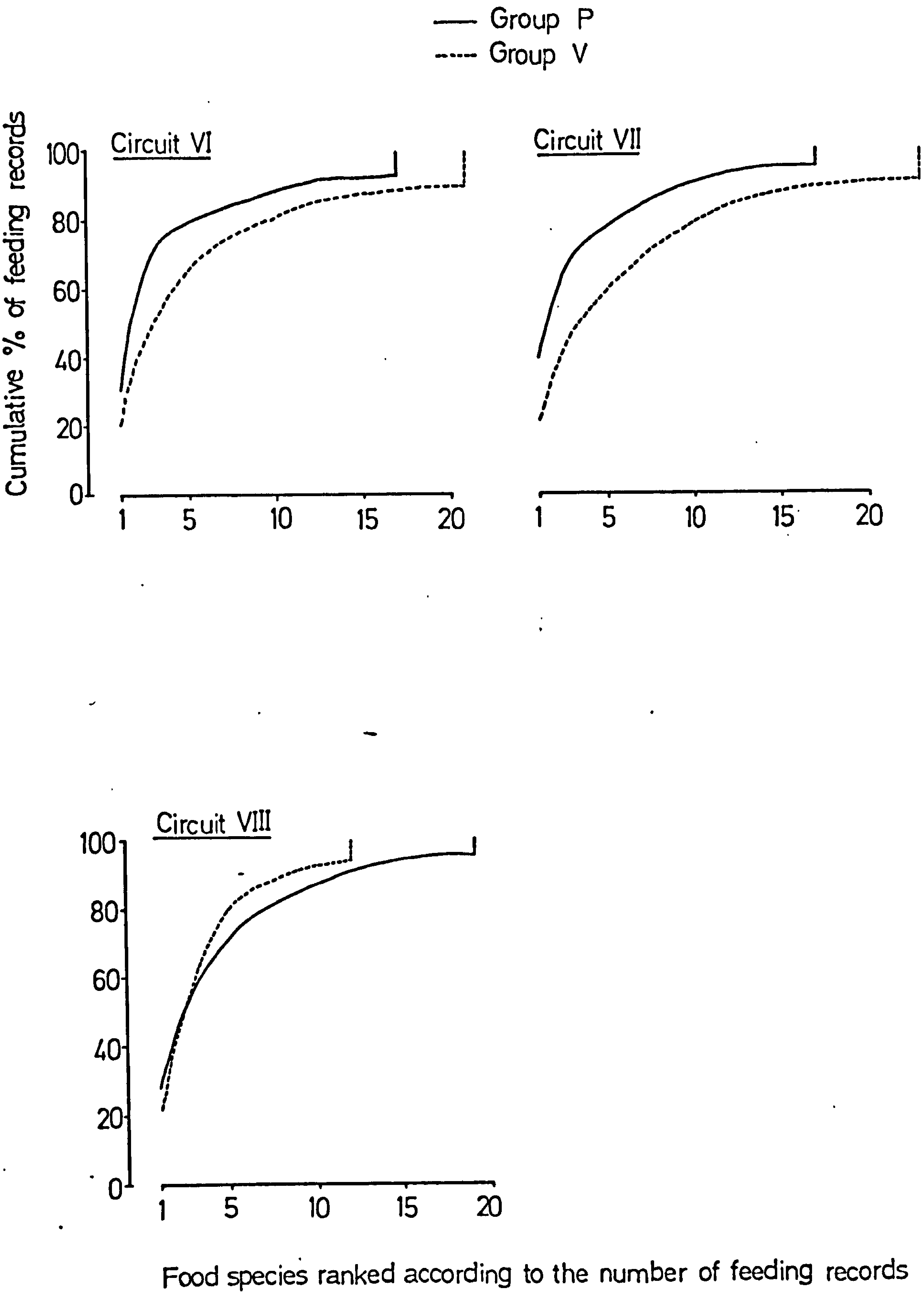
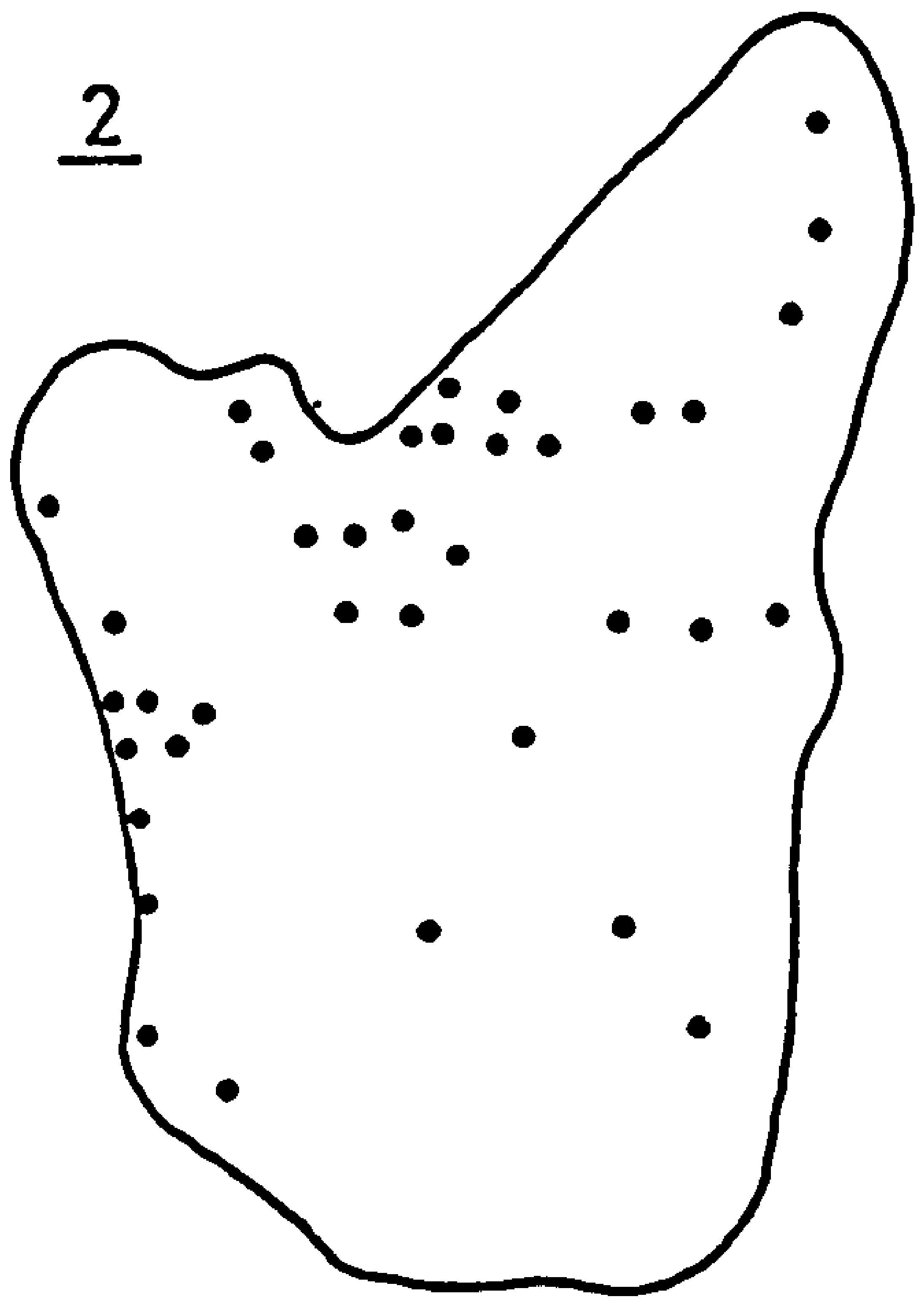

Group P
Group V
Cumulative % of feeding records
Circuit VI
100
80
60
40
20
0
1
5
10
15
20
Circuit VII
1
5
10
15
20
Circuit VIII
100
80
60
40
20
0
1
5
10
15
20
Food species ranked according to the number of feeding records

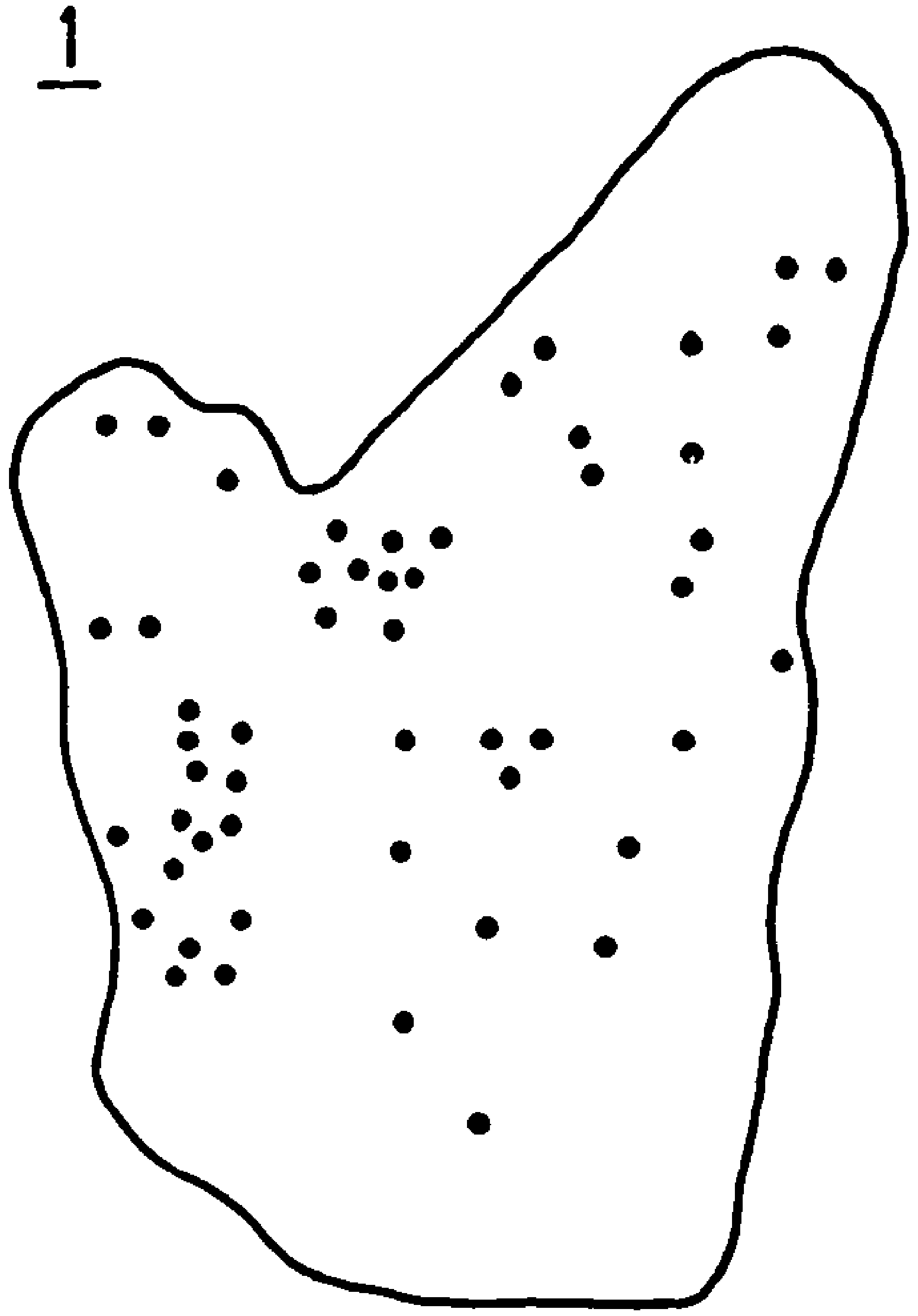
Figure 6.12 Spatial distribution of major foods. Each spot represents 30 minutes of feeding over the year on major food species in the home ranges of Group P and Group V. The top-ranking 5 species for Group P and top-ranking 3 species for group V are illustrated.

2



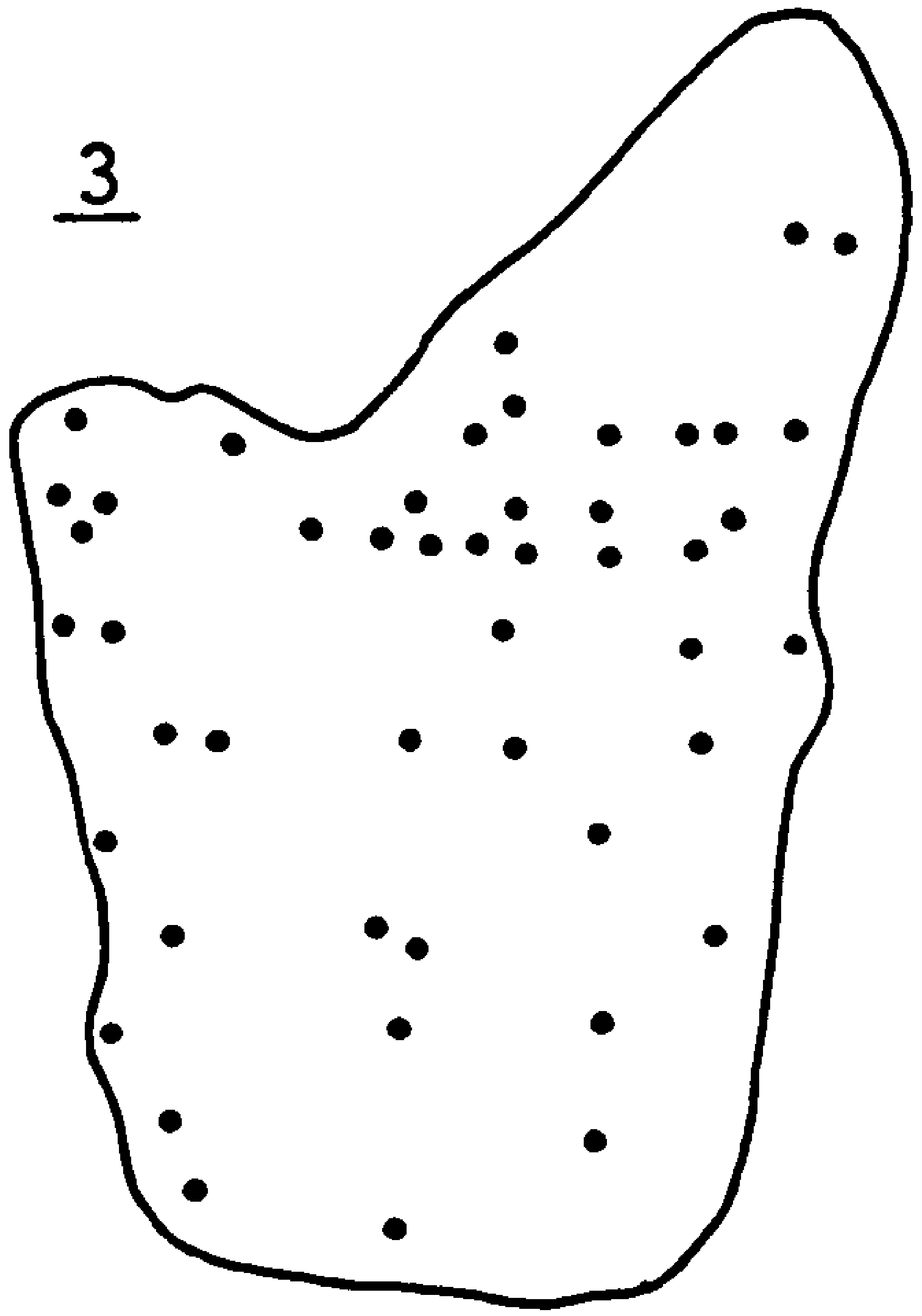
Species 44

1



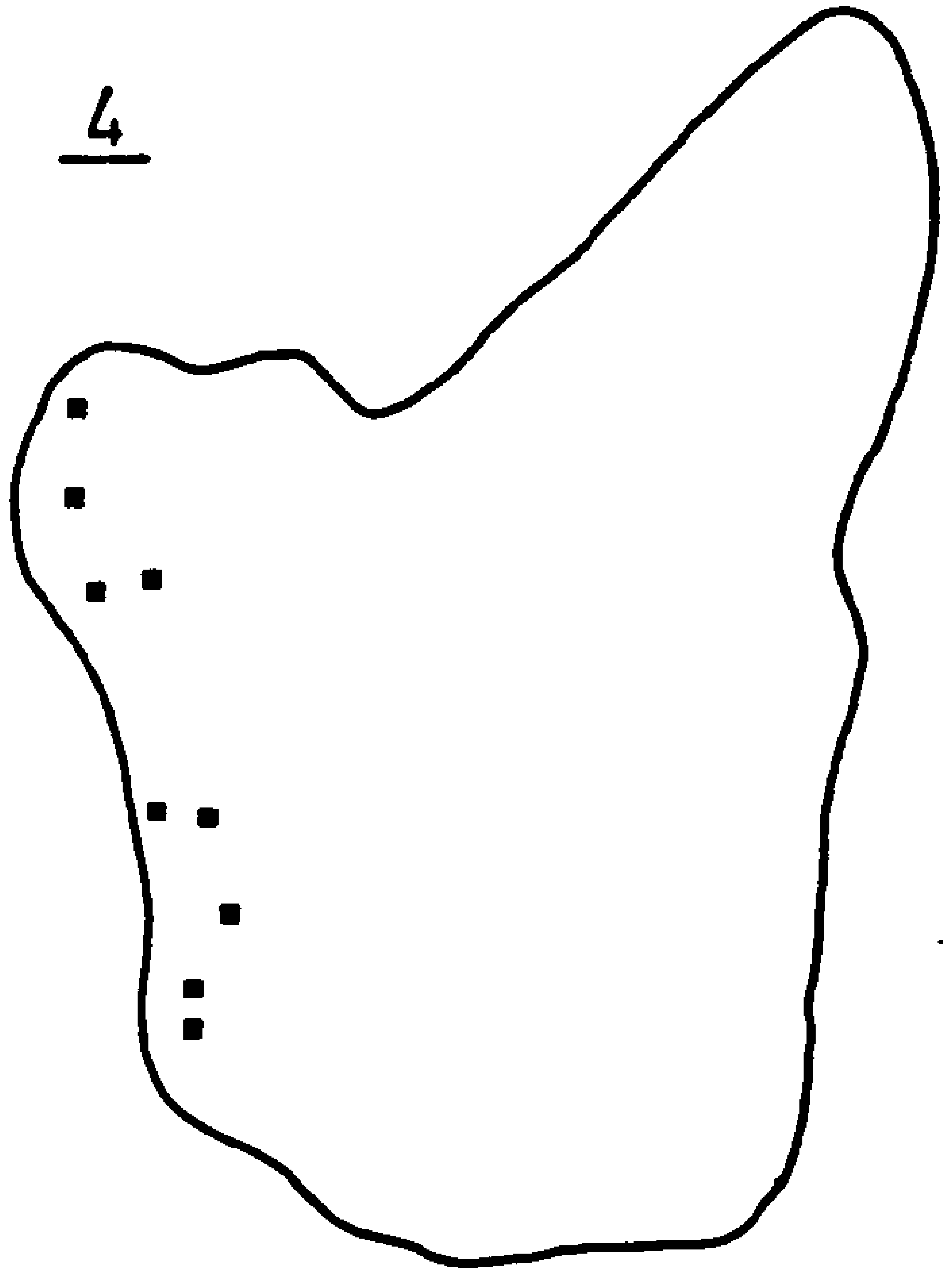
Species 39

3



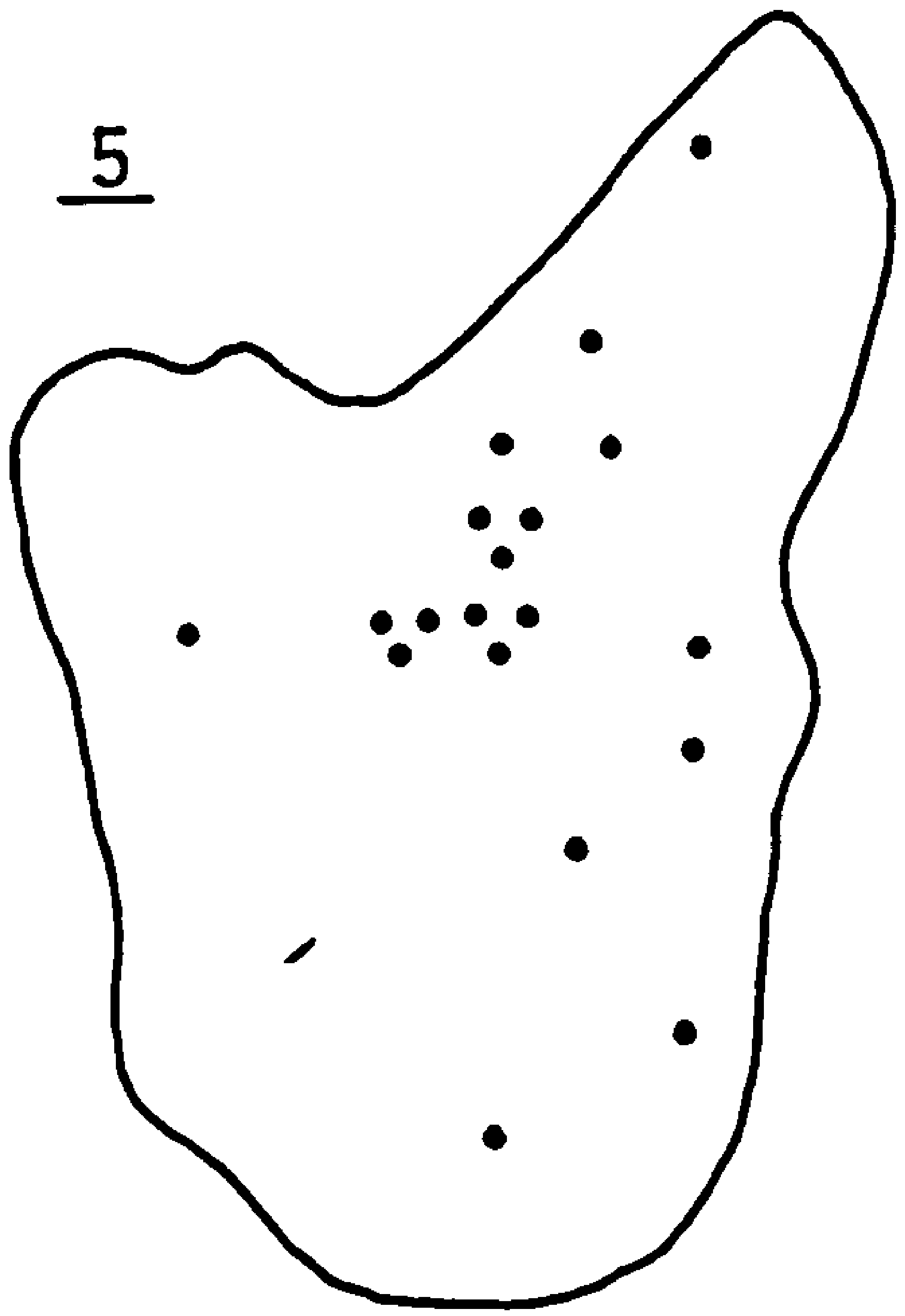
Species 48+50

4



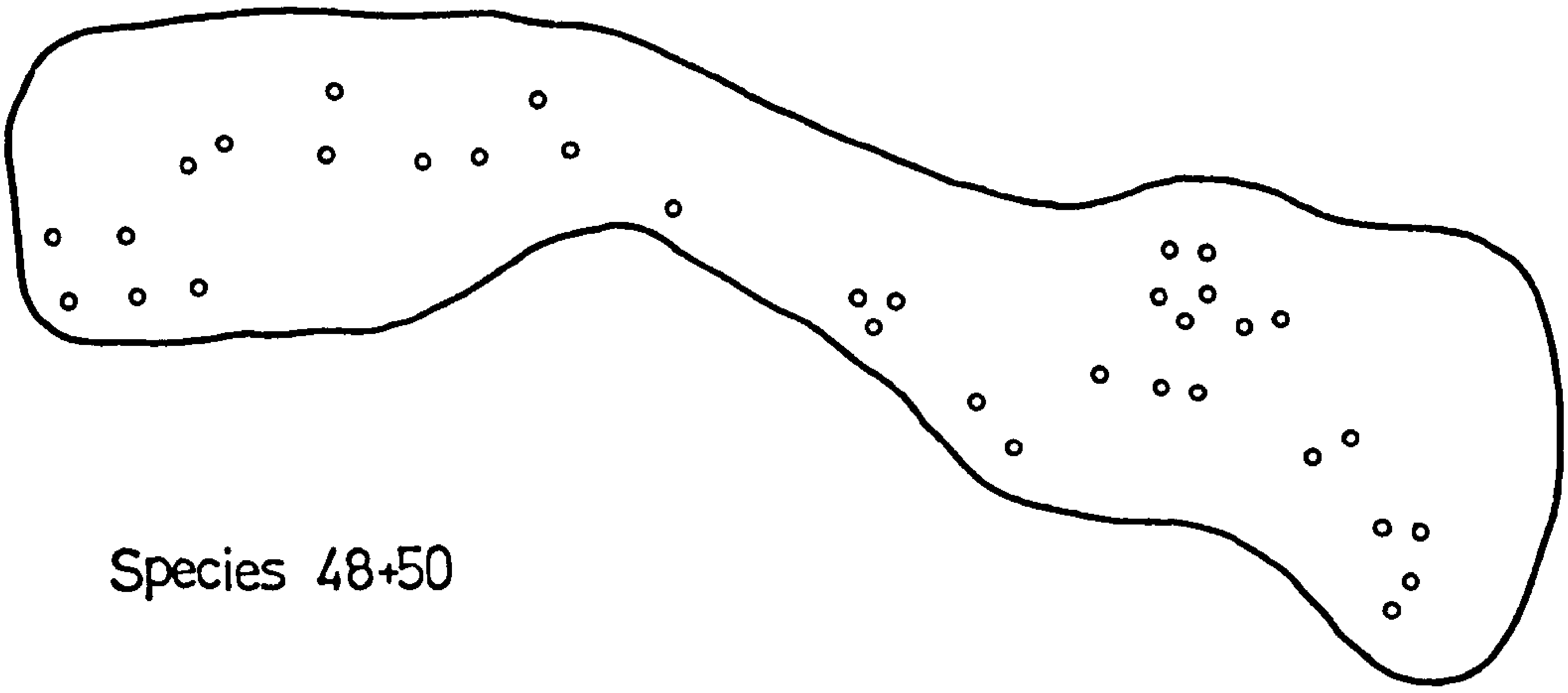
Species 45

5



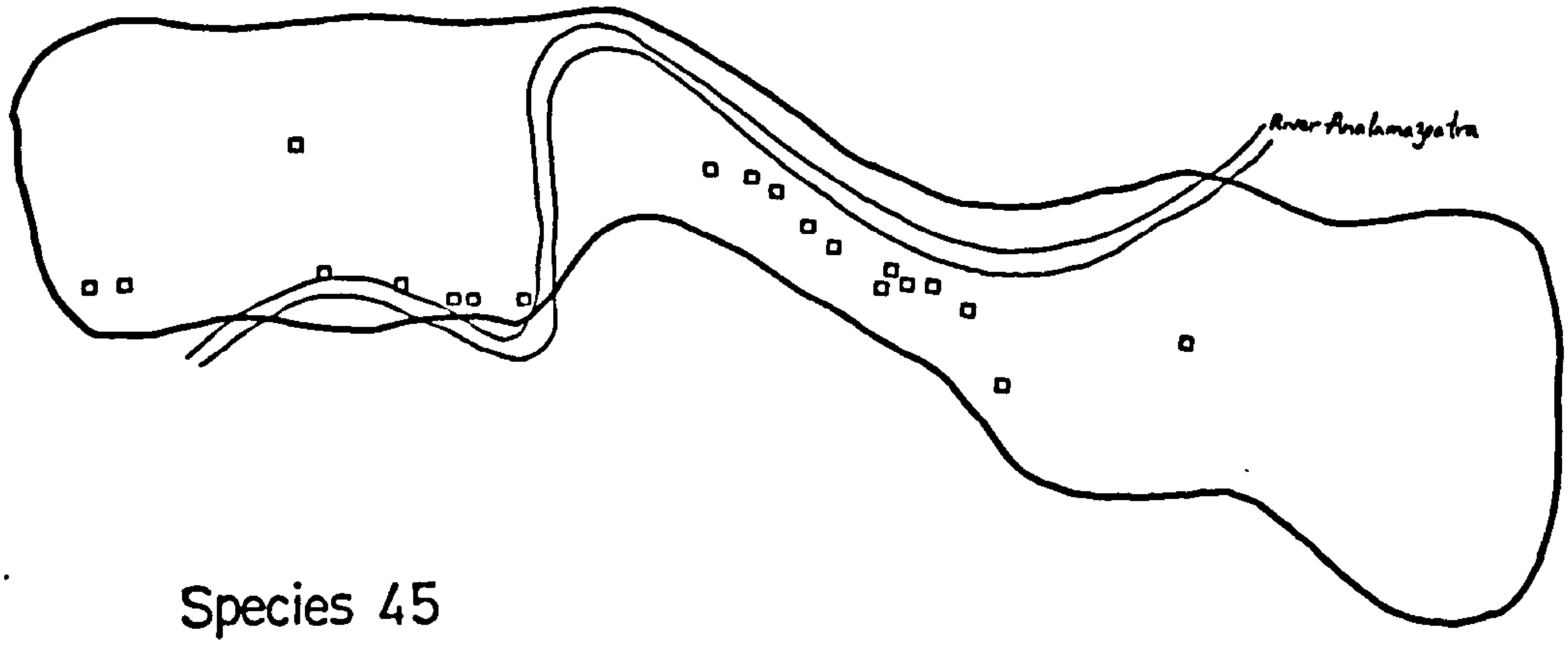
Species 2

2



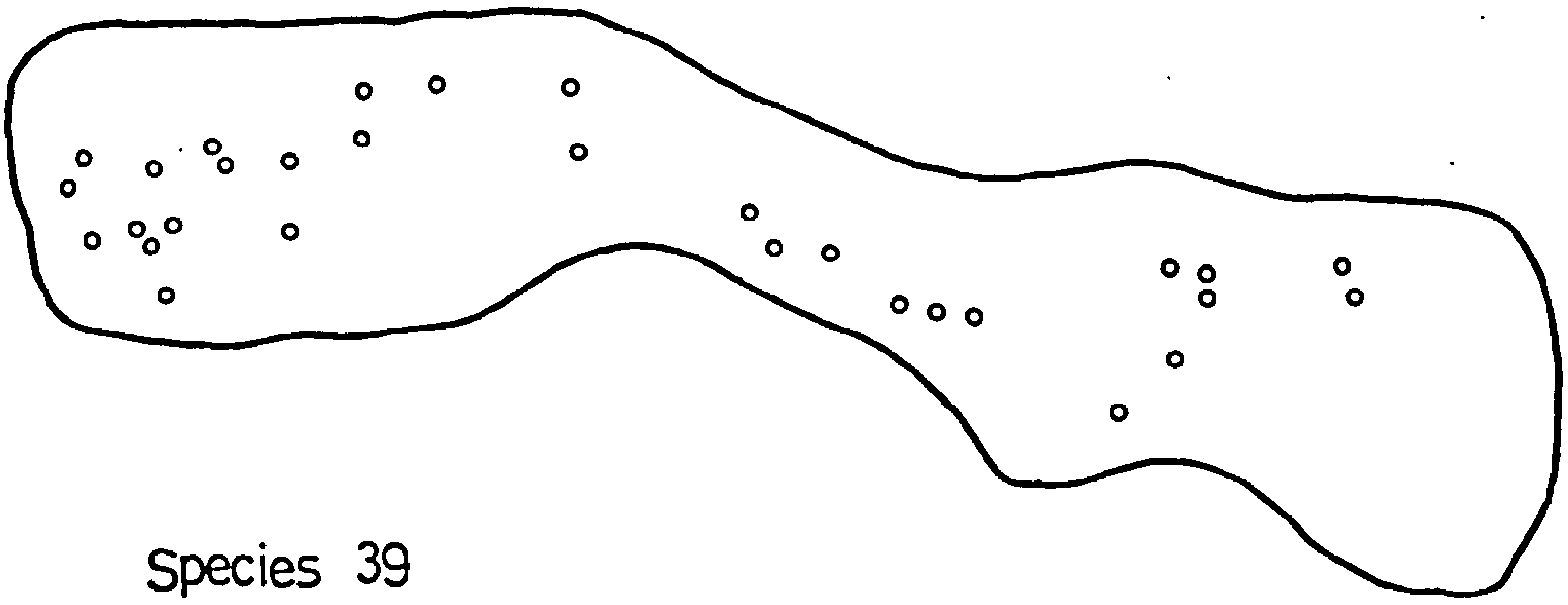
Species 48+50

1



Species 45

3



Species 39

Circuit III the seeds of unripe fruit were consumed, by Circuit IV the kernel had hardened and the pericarp was gnawed and in Circuit VII, the fruiting having finished, the trees sprouted new foliage which was eaten. In Group P's home range less than a dozen individuals of the species existed and these were all situated in a low, moist part of the home range, growing on the banks of the River Analamazoatra and its tributaries.

(b) Group V

The periods of observation on this group were not long enough to plot important food locations unless they were consumed throughout the year. This restricted the examination to only 2 species: Ocotea sp. and Ravensara pervillei which appeared to be eaten in all parts of the home range (Fig. 6.12).

Cryptocarya olseodaphnifolia was found, as in Group P, to be eaten from a few individual trees situated by the edge of the river. It is unlikely that this species grew elsewhere in either group's home range.

Some food e.g. Uapaca bojeri was clumped in the forest and the animals would move to these areas, sometimes on long progressions, in order to feed on specific individual trees, especially if these were fruiting. Other species were eaten everywhere and these tended to be the food most often chosen, both for overall quantity and for their selection at all times of the year.

8. INDIVIDUAL VARIATION

Individuals varied widely in all aspects of feeding behaviour. These included the overall time spent feeding, rate of food consumption and, to a lesser extent, the type of food consumed.

8.1. Feeding rate.

Only observations of feeding on certain fruits, which could be easily scored as their remains fell to the ground, suggested differences between individuals in the rate of feeding. The adult female of Group V consistently fed more rapidly on the fruit of Ravensara sp. than the adult male (Mann-Whitney U test; $p<0.02$).

There are insufficient data to compare other individuals but in general feeding rate appeared to be greatest in those individuals which fed longest (see below) thus enhancing rather than balancing individual variation in the quantities of food consumed.

8.2. The time spent feeding.

8.2.1. Overall differences.

Although the degree to which individuals differed in the amount of time spent feeding was complicated by seasonal variation (see below) tests of individual variation in Group P established 3 important results (Table 6.4). Firstly, the adult male fed significantly less (i.e. less by time) than every other group member; secondly, the youngest individual fed significantly more than every other group

	Ad♂	O3	O2	O1
Ad♀	19.102 <0.001 ***	1.318 <0.3 >0.2	1.069 <0.5 >0.3	5.651 <0.02 >0.01 **
	Ad♂	9.791 <0.001 ***	27.29 <0.001 ***	43.982 <0.001 ***
		O3	4.425 <0.05 *	11.794 <0.001 ***
			O2	1.572 <0.3 >0.2

	Ad♀	Ad♂	O3	O2	O1
% feeding	52.8	42.1	50.0	55.4	58.7
$\bar{n}$ (15' records)	878	766	764	760	858

TABLE 6.4. % time spent feeding by each individual in Group P throughout the year, with $X^2_{(1df)}$ values comparing individuals.

	Ad ♀	Ad ♂
% feeding records	51.3	34.0
n (15 min. records)	915	806
$X^2_{(1df)}$	52.3	
p	<0.001	

TABLE 6.5. % time spent feeding by each adult in Group V throughout the year.

member except the next youngest individual; and thirdly, the oldest, adult-sized offspring fed significantly less than the two youngest offspring.

As in Group P, the adult male of Group V spent very much less time feeding than the group's adult female (Table 6.5).

Comparing the real rather than the proportionate amount of time spent feeding by the adult females of each group failed to demonstrate significant differences between them ($0.5<p<0.7$) but illustrated the fewer feeding records obtained for the Group V adult male compared to his Group P counterpart ($0.001<p<0.01$).

8.2.2. Seasonal differences.

The seasonal distributions of individuals' feeding activities (Fig. 6.13) were examined by comparing each individual with each member of the same group for every Circuit.

(a) Group P

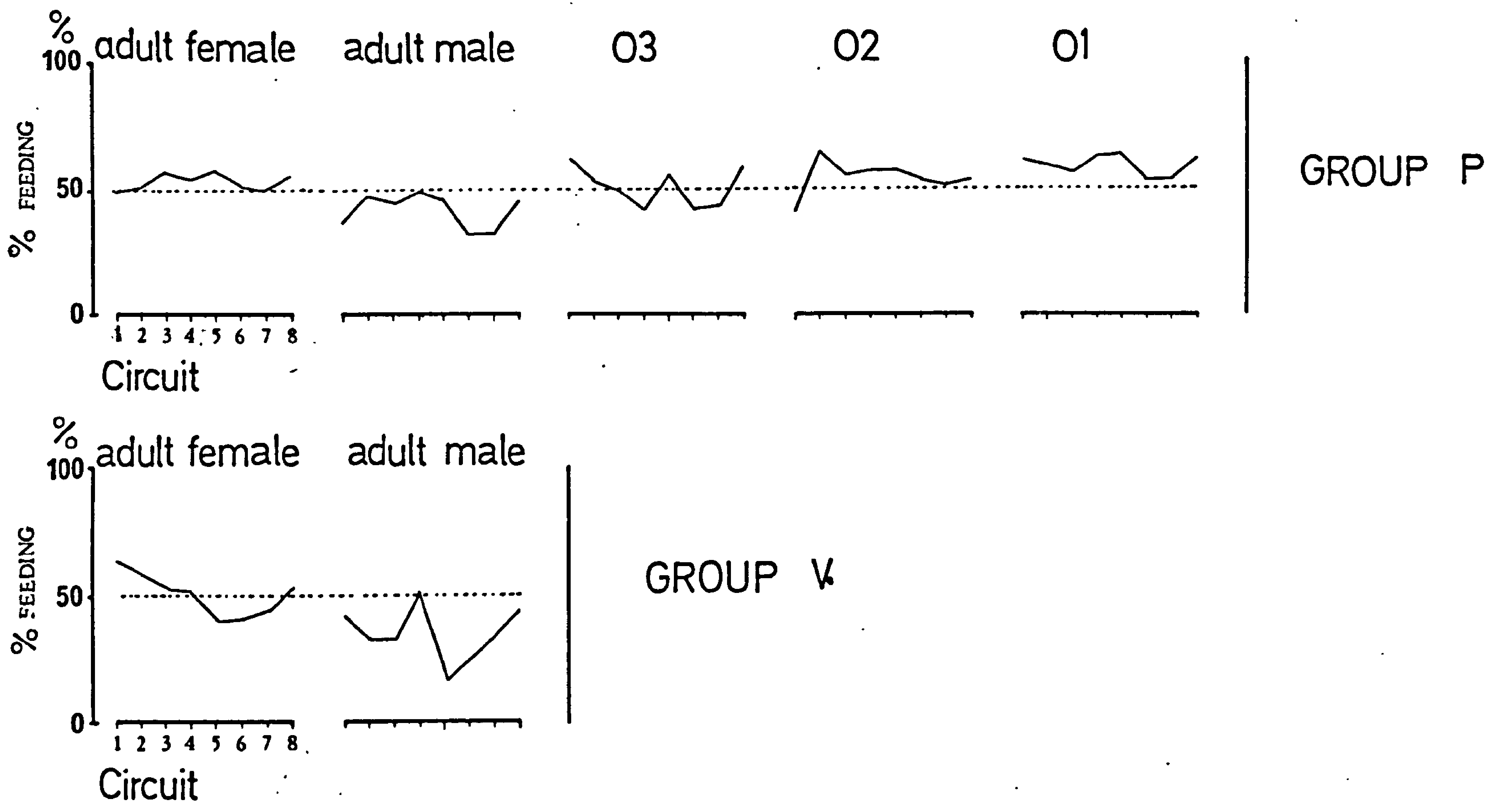
From the 80 tests there were 17 significant differences, 13 of which described the adult male's relatively poor level of feeding. There was no common pattern of seasonal change in the way the time each individual spent feeding varied relative to others in the group.

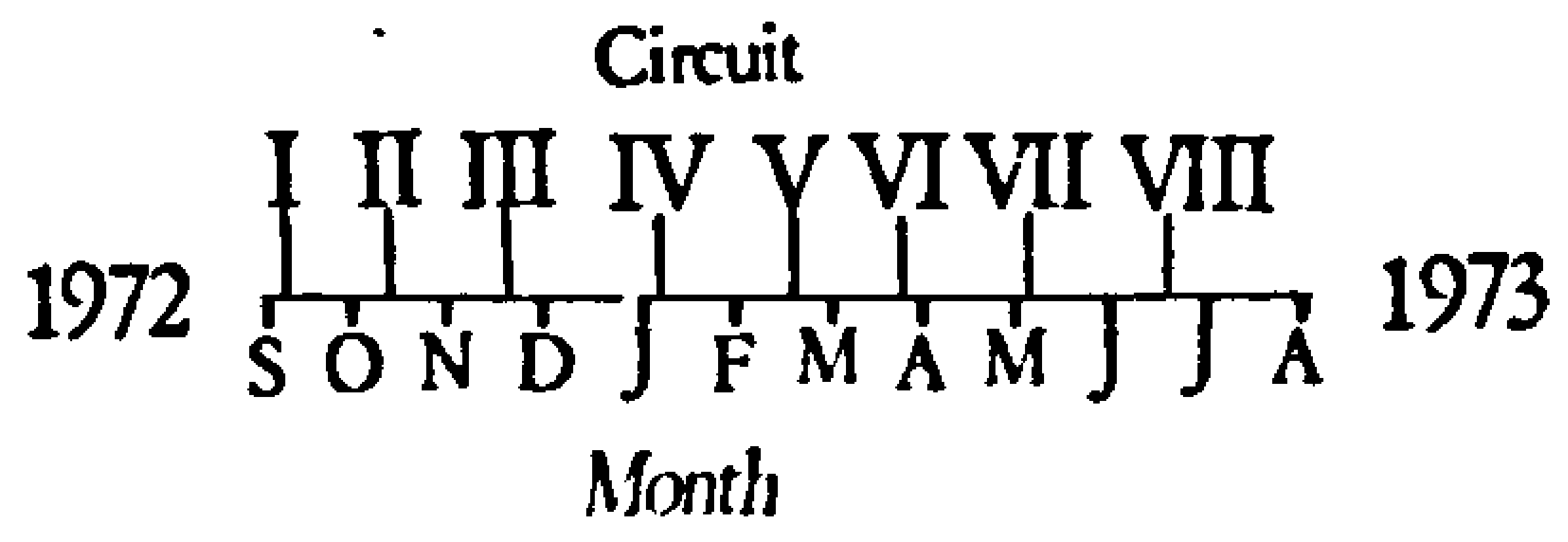
During Circuits VI and VII, the time when the group as a whole fed least, a considerable reduction occurred in the numbers of feeding records obtained for the adult male.

(b) Group V

The adult male of Group V fed significantly less than

Figure 6.13 Seasonal distributions of the proportion of time spent feeding by each individual in Group P and Group V.


%
100
50
0
% FEEDING
adult female
adult male
O3
O2
O1
GROUP P
1 2 3 4 5 6 7 8
Circuit
%
100
50
0
% FEEDING
adult female
adult male
GROUP V
1 2 3 4 5 6 7 8
Circuit


Circuit
I II III IV V VI VII VIII
1972
S O N D J F M A M J J A
1973
Month

the adult female for Circuits I, II, and III. The probability of further significant differences was high but the small sample sizes reduced the power of statistical comparison.

During Circuit V, a considerable reduction occurred in the adult male's feeding records and this was the time when the group as a whole fed least.

8.3. The type of food consumed.

Competition between group members might have caused individuals to feed differently. It has been already shown that individuals differed in the amount of time they were feeding and in their position in trees and this might be expected to influence the composition of their diet.

8.3.1. Food species.

No obvious differences in the amount of time different individuals spent feeding on the same species were evident. However, a cursory examination of individual differences in the amount of time spent on different species was performed. Sample size limitations restricted the analysis to major food items.

In Group P the species most consumed overall, Ocotea sp., was eaten less by the adult male than by either O3 ($X^2_{1df} = 4.04$, $0.01<p<0.05$) or O1 ($X^2_{1df} = 6.41$, $0.01<p<0.05$) individuals. O1 also fed significantly more ($X^2_{1df} = 5.32$, $0.01<p<0.05$) than O2 on this species. Ravensara pervillei, the second ranking food, was consumed equally by individuals of the group. In Group V the top two ranking species were eaten equally by the two adults.

8.3.2. Food parts.

Individual preferences for (i) fruit and (ii) young leaves were examined. No differences were found within Group P, but the adult female of Group V fed on young leaves for 37.9% of the time compared to the adult male's 19.1% ($X^2_{1df} = 13.32$, $p<0.001$).

The adult male of Group V fed proportionately significantly more on fruit than any member of Group P ($X^2_{1df(min)} = 5.4$, $0.01<p<0.05$). The Group V adult female fed proportionately significantly more on young foliage than any member of Group P ($X^2_{1df(min)} = 4.314$; $0.01<p<0.05$).

Adult males therefore fed for less time, may have consumed food more slowly and appeared to eat more fruit and less shoots than adult females and young offspring. In addition the adult male of Group V fed far less than any other individual in either group.

9. FEEDING AND RANGING BEHAVIOUR

9.1. Ranging for food.

The pattern of movement about the home range seemingly depended only on the distribution of food (see Chapter 7). When a desirable species or group of individual trees were fruiting or growing new foliage, *Indri* made early progressions to the food source (usually from a near central sleeping location) which were followed by a bout of intense feeding, with very little movement, for 2 to

3 hours. The remainder of the day was then devoted to sequences of short progressions and feeding bouts on a diverse array of suitable species. Ranging patterns, in this case, reflected the repeated use of small parts of the home range and the specific arboreal pathways separating them.

When no concentrated food source was available, shorter feeding bouts interrupted by small progressions took place. Occasionally a group would travel 200-300 metres in one long movement taking them diametrically across their home range. A more even utilisation of the home range occurred at these times.

9.2. Home range utilisation and feeding.

Despite concentrating equally on similarly sized portions of their home ranges (see below), the two study groups differed in the way different quadrats were used. Group V spent relatively less time per entry in low ranking quadrats (quadrats in which only small overall amounts of time were spent) than in high ranking quadrats. This relationship was absent in Group P, which appeared to use equally the quadrats it did visit (Figure 7.5). There was no relationship between the time spent in a quadrat and the proportion of time spent feeding in that quadrat.

Both groups, whilst adopting different strategies, appeared to revisit parts they knew contained food. In Group P, for example, the amount of time spent in a quadrat was not significantly correlated with the number of species consumed in that quadrat ($r^s = 0.0935$, $t = 0.42$; $0.6<p<0.7$), and this group therefore appeared to be entering specific quadrats in order to feed on specific foods[1]. The movements of Group V[2], however, spending relatively small amounts of time in little used quadrats each time they were entered suggested that they were concentrating on parts of the home range they knew contained food, whilst rapidly passing through other areas.

9.3. Local movements and feeding.

The impression that Group P's ranging movements each day were organised into a definite pattern was gained from observations of their tendency to travel in straight lines or wide arcs. Measures of the acuteness of turns performed by each group each Circuit (Fig.7.17)[3] were found to be correlated with the proportion of time spent feeding in Group V ($r^s = 0.75$, $0.01<p<0.05$) but not in Group P ($r^s = 0.07$). Attempts to correlate each group's angled movements with each adult's time spent feeding isolated the adult male of Group V as the main contributor to his group's variation in this measure ($r^s = 0.82$, $0.01<p<0.05$). The Group V male was thus feeding least when most angled movements were being taken by the group.

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[1] As many infrequently used quadrats would have conferred an artificial significance to the data, only the top twenty ranking quadrats were considered.

[2] The observation periods in Group V were of insufficient length to properly rank the numbers of plant species consumed in each quadrat.

[3] Although no overall difference in the frequency of angled turns was found between groups, the longer shape of Group V's territory suggests that this group had a reduced opportunity for turning acutely.

Furthermore, the frequency with which individuals in Group V moved to a new tree was three times that of Group P and longitudinal observations of the Group V adult male and the Group P adult female showed that the former made about three times as many jumps as the latter every day (see Chapter 7).

The tendency for Group V to move more rapidly through rarely visited quadrats, to move more within quadrats than Group P, and to make most angled turns when they fed least, all implied a poorer knowledge of food location than Group P or a dearth of food in certain parts of their home range. Years of accumulating experience may precede a proper knowledge of the whereabouts of food.

The composition of the group, the probable recent acquisition of Group V's territory[1] (according to the local people), and the seemingly satisfactory levels of food observed in all parts of the forest when the animals fed little, suggest the former interpretation.

10. FEEDING BEHAVIOUR AND SOCIAL BEHAVIOUR

10.1. Introduction.

The social effect, be it inhibitory or facilitatory, of one individual on another's feeding activities can be partially examined by considering (i) which individuals by their presence affect the proportion of time other group members spend in various activities, and (ii) to what extent other individuals affect the temporal synchrony of

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[1] see Chapter 9.

activity within the group. In this study the *presence* of other group members could not be shown to radically affect the proportion of time that individuals fed, because animals tended to aggregate in dense food sources, but differences in the relative timing of activity between some animals were obvious.

10.2. Behavioural 'synchrony' between adults.

Normally, the degree of activity synchrony within *Indri* groups is high as animals tend to rest, move and feed together. Observed measures of synchrony of 'feeding' and 'other' activities between adults in each group were compared to those expected by chance. Activity synchrony was found to be significant in Group P for both 'feeding' and 'other' behaviours, but did not differ significantly from chance in Group V (Table 6.6). The organisation of adults' behaviour in Group V was further investigated as it appeared unlikely that group members could behave as independent entities in an essentially cohesive group. The proportion of time spent feeding by the adult male of each group during each Circuit was calculated for (i) those times when the adult female of his group was *feeding* simultaneously, and, (ii) those times that the adult female was *not feeding* simultaneously (Fig. 6.14). The proportion of time spent feeding by the Group V adult male when the group's adult female was *feeding* was found, over the year, to be positively correlated with the *overall* proportion of time spent feeding by the adult male, irrespective of his female's activity ($r^s = 0.91$, $p<0.001$).

	GROUP P				GROUP V			
	Ad♀F		Ad♀NF		Ad♀F		Ad♀NF	
	Ad♂F	Ad♂NF	Ad♂F	Ad♂NF	Ad♂F	Ad♂NF	Ad♂F	Ad♂NF
Observed	148	93	34	130	156	233	90	195
Expected	108.2	132.8	73.6	90.4	141.9	246.9	104.1	181.0
x^2	13.198		21.689		1.07		1.545	
p>	0.001		0.001		0.33		0.22	

F - Feeding NF - Not feeding

TABLE 6.6. Synchrony in behaviour between adults of each group.

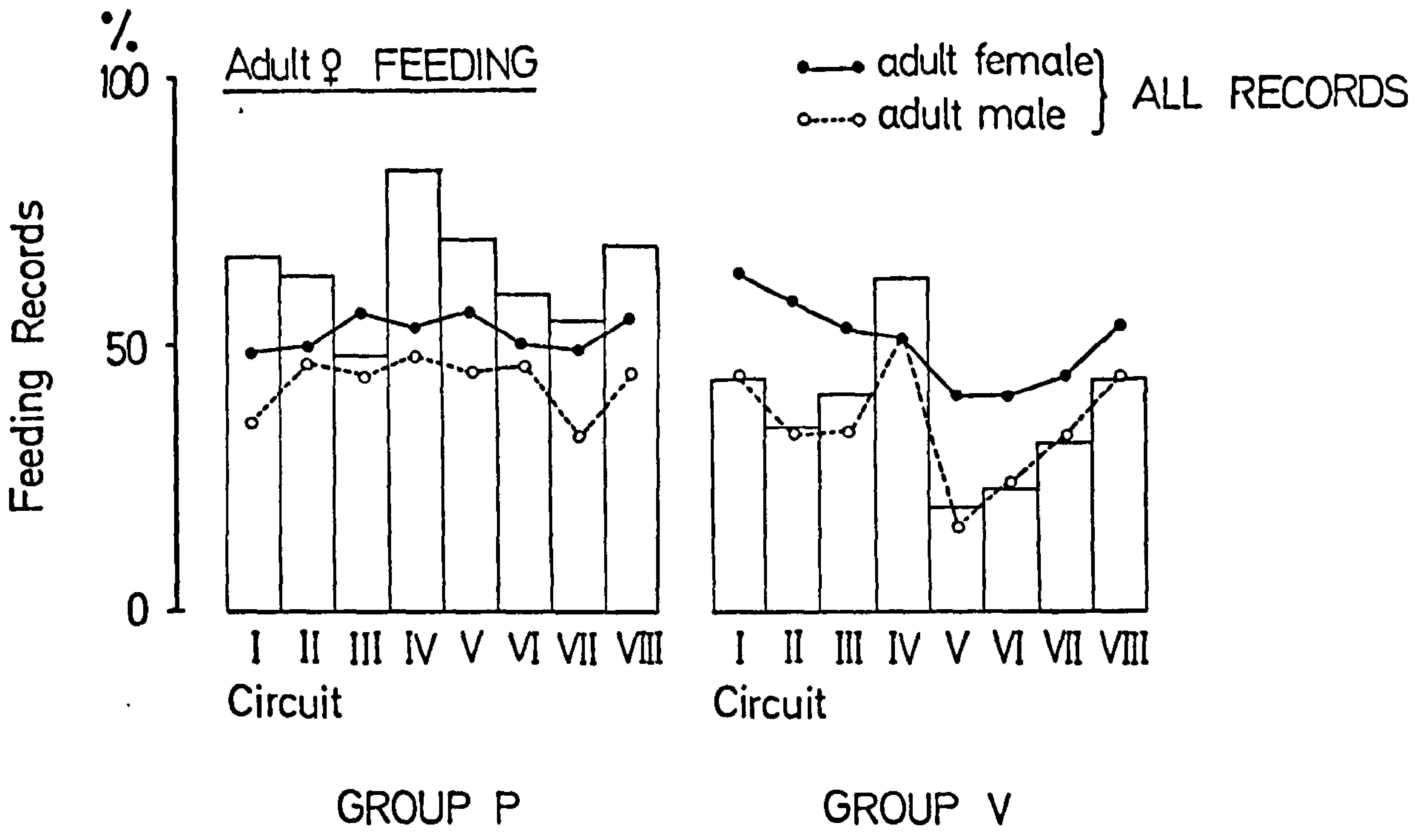
OBJECT

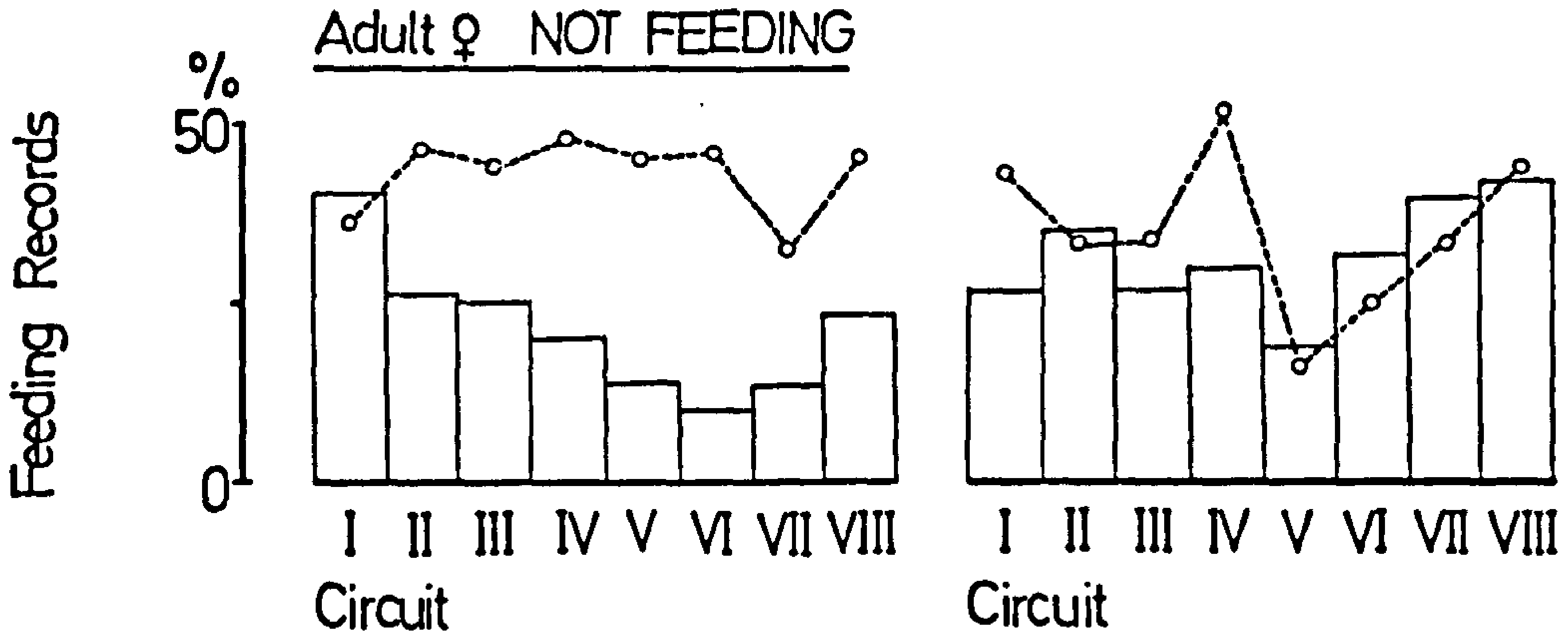
SUBJECT	Ad♀	Ad♂	03	02	01
Ad♀	-	61.4	71.2	74.9	80.2
Ad♂	81.3	-	74.7	82.3	84.2
03	79.5	68.1	-	81.7	80.2
02	79.5	67.1	73.3	-	81.1
01	75.8	63.4	69.0	74.6	-

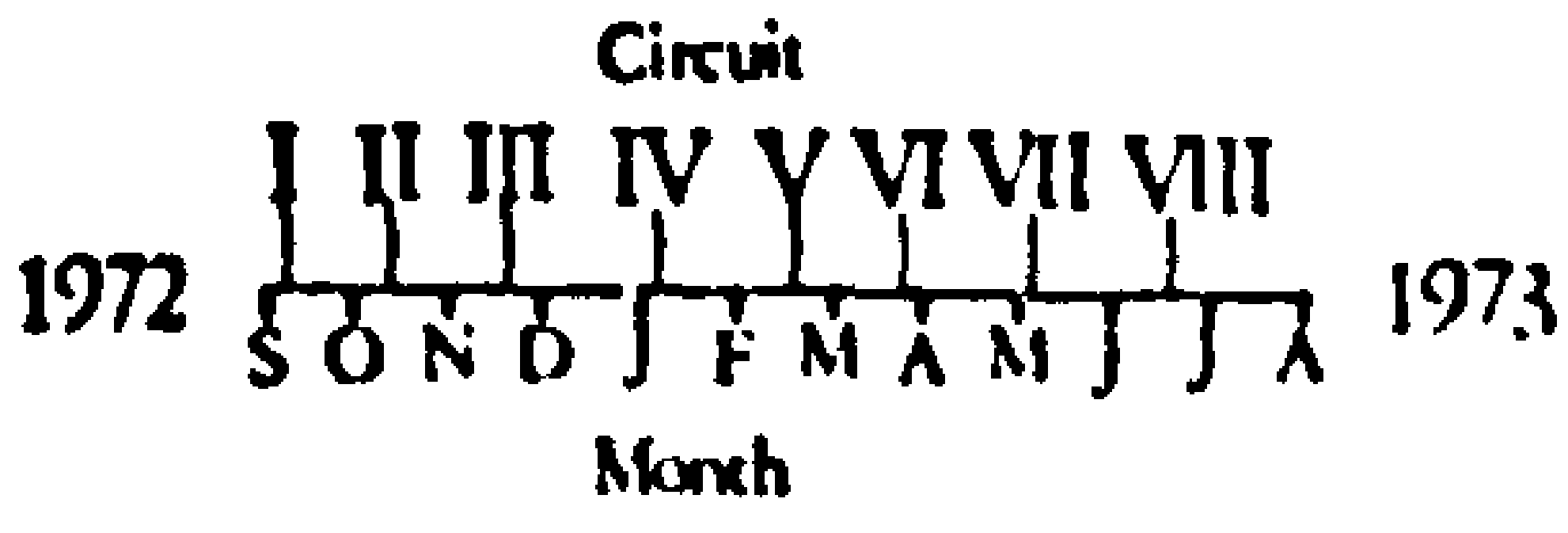
TABLE 6.7. Percentage of objects records that each was seen feeding when subject was feeding.

Figure 6.14 Seasonal variation in activity synchrony between adults in Group P and Group V.

Each histogram represents the proportion of records of feeding by the adult male when the adult female was (1) feeding, and (2) not feeding, for each Circuit. Also illustrated is the total % time spent feeding by each adult during each Circuit.


Adult ♀ FEEDING


Adult ♀ NOT FEEDING



There was no such relationship between the adult male and female of Group P ($r^S = 0.14$; $p>0.1$).

The proportion of time spent feeding by the adult male when the female was engaged in activities other than feeding was not significantly correlated with the amount of time spent feeding overall by the adult male either in Group V ($r^S = 0.17$) or Group P ($r^S = 0.05$).

The amount of food consumed by the adult male of Group V appears not only to be correlated with, but to be directed by, the amount of time he fed simultaneously with the adult female. This effect is absent in Group P. That this 'direction' came from the adult female is in no doubt as she frequently and actively forced the adult male to move from feeding positions (which she would then occupy), whereas he was never seen to aggressively approach or displace her. Having been moved the adult male would usually rest low in the forest whilst the female fed in the canopy (see Chapter 5).

Activity 'independence' of the Group V adults (Table 6.6)is thus seen to be an artefact consisting both of organised synchrony and asynchrony of behaviour which integrate to an apparently random consistency. The lack of a strong inhibitory effect on the adult male's feeding behaviour in Group P explains the expected high degree of intra-group behavioural synchrony.

The discovery of differences in activity synchrony between the adult pairs of each group encouraged further examination of behavioural dependence in the large group

(Group P) with a view to supplying more evidence for the presence of discrete expressions of feeding relationships between individuals.

For each pair of animals, both individuals' activities ('feeding' and 'other') were represented as percentages of the time they were seen together. Tables were drawn depicting the proportion of time each individual was feeding when seen to be near[1] every other group member when the latter was (a) feeding and (b) not feeding.

10.3. Behavioural synchrony in Group P.

The high degree of feeding synchrony (Table 6.7) is shown by the greater percentage of feeding records occurring for every individual in the presence of every other group member, compared to their overall individual feeding records percentages. Conversely, the percentage of time spent feeding when individuals nearby are engaged in activities other than feeding is, in every case, less than the overall individual feeding record percentages (Table 6.8).

10.4. Feeding relationships in Group P.

10.4.1. Feeding synchrony (Table 6.7).

The numbers of records of (i) feeding and (ii) not feeding, for each subject when near[1] to every other group member, were calculated. These were then statistically compared for each pair of animals against every other pair.

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[1] "near", here, refers to two animals being simultaneously sighted. This usually meant that the two animals were within 10 to 15 metres of each other.

OBJECT

SUBJECT	Ad♀	Ad♂	03	02	01
Ad♀	-	21.0	27.4	31.3	34.0
Ad♂	42.1	-	37.7	41.7	42.4
03	37.1	30.3	-	38.5	48.1
02	37.2	23.9	27.7	-	39.2
01	28.6	19.4	33.8	30.7	-

TABLE 6.8. Percentage of object's records that each was seen feeding when the subject was not feeding.

	Ad♀	Ad♂	03	02	01	n
1st	1	15	0	1	2	19
2nd	2	1	0	9	6	18
3rd	4	3	2	3	4	16
4th	1	0	6	2	2	11
5th	2	0	4	1	2	9
Total	10	19	12	16	16	73

TABLE 6.9. Individual differences in departure order from trees from which all Group P members fed.

Only one significant difference was encountered - the greater proportion of time spent feeding by O2 in the presence of the adult male (82.3%) compared with O2 in the presence of O1 (74.6%; $X^2_{1df} = 3.8419$; $p = 0.05$).

10.4.2. Feeding asynchrony (Table 6.8)

As Table 6.8 contains instances when all group members were feeding on a single dense food source, the effects of different dyadic relationships on feeding activities may be concealed. These effects, if present, would be exposed by a controlling measure - that of individual variation in feeding when different subjects were near to an individual who was not feeding. Here, statistically significant differences involved every individual[1]:

(i) The adult female fed more in the presence of the adult male* than O1.*

(ii) The adult male fed more in the presence of O3* than O1.*

(iii) O3 fed more in the presence of the adult male* than the adult female.*

(iv) O2 fed more in the presence of the adult male* than O1.*

(v) O1 fed more in the presence of the O3* individual than the adult female.*

The polarity of these results is consistent. Firstly, where there are differences, each individual fed more when seen near to non-feeding adult male or O3 individuals.

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*when these individuals were not feeding.

[1] X^2_{1df} values: (i) 8.74, $0.001<p<0.01$; (ii) 5.001, $0.01<p<0.05$
(iii) 3.97, $0.01<p<0.05$; (iv) 4.46, $0.01<p<0.05$
(v) 8.37, $0.001<p<0.01$

only. Secondly, where there are differences, each individual fed less when seen near to non-feeding O1 or adult female individuals only. Just as in every case the percentage time spent feeding by individuals was always greatest when the adult male was in view and feeding (Table 6.7), in only one case was this no longer true when the adult male was in view and not feeding. Thirdly, the only difference found in measures of "feeding synchrony" (above) is also seen in "feeding asynchrony" measures: the O2 animal feeding significantly more than O1 when each was seen with the adult male, irrespective of the latter's activity.

Because the adult male and O3 animals fed slightly less when no other group members were seen to be near them (42.3% and 48.3% respectively) compared to overall proportions of time they spent feeding (45.3% and 51.6% respectively), these results can not be explained by the possibility that these individuals were feeding more in asocial situations, and approaching other animals only when they had sufficiently eaten. A preferred explanation is that locally acting inhibitory effects, produced by the presence of close individuals, caused them to alter their feeding behaviour according to the presence or absence of others. The origin of these influences can only be determined by consideration of social interactions between specified individuals (see Chapter 8).

The above analysis was restricted to dyadic situations, whereas the combined effect of several individuals may specifically evoke behavioural changes in others. Larger animal aggregations tend, however, to occur in dense food sources and require longer inter-sample intervals which thereby reduce the quantity of data and prohibit statistical examination.

Consideration of aggregations of 4 animals, however, suggest that (a) the adult male fed more when the female was absent (53.5%) than when she was present (37.2%), and, (b) that 03 fed more when the adult male was absent (66.0%) than when he was present (53.2%). These differences were not significant, although sample size was small and the probability of Type II errors great.

It is probable, therefore, that continuous elements of social communication, not evident to the observer, influenced social configurations of feeding animals in Group P. These were namely that (i) animals were more likely to be feeding when the adult male and 03 individuals were <u>not</u> feeding (facilitation), and (ii) that the presence of 01 and the adult female exerted a mild but clear inhibitory effect on other's feeding activities, which showed through the high level of behavioural synchrony within the group. In no case, however, did the degree to which one member of Group P influenced the behaviour of another compare with the feeding discipline exerted on the adult male of Group V by that group's adult female.

10.5. Feeding orders and movements.

The observer was often unable to stay close to leading members of the group during rapid progressions. As a result the first animals entering a tree could not be seen and the order in which animals left a large food source were preferentially recorded to those of entry. Individual differences existed, however, in this measure (Table 6.9): the adult male of Group P leaving first on 79% of observations of his position in the departure order. In Group IV at Vohidrazana an adult-sized female was consistently the last to enter and leave feeding trees in which all animals fed, and always brought up the rear in group progressions. To a lesser extent this was also true of the O3 individual in Group P at Analamazoatra (Table 6.9)who was recorded as last in group progressions 44% of the time. O3, the oldest adult-sized offspring, was the animal most often displaced from feeding positions (38.3% of all displacements) by all other group members and the least often groomed (10.3% of all allogrooming interactions).

In Group V each adult appeared to equally share the role of progression leader, but as the direction of movements were often reversed and as animals often overtook each other, the 'leader' was often difficult to define. In Group IV, shortly after the birth of an infant in May 1973, it was the adult female who consistently directed movements to new food sources, being essentially followed around the home range by other group members.

11. DISCUSSION

Social dominance, exerted primarily in feeding contexts, clearly differentiated the adult females and young animals from other individuals. They fed more, and not only had priority of access to food, but could also (at least in some cases) determine group movements and effectively control the amount that others fed. Adult males fed least of all, fed relatively more in structural rather than food-bearing parts of the trees, and were easily displaced from feeding positions. As discussed in Chapter 9 the adult males also took most responsibility for group defence by participating actively in the repulsion of invading groups from their territory, whilst the adult female (and others) rested in a safe central location .

Adaptive facets of Indri feeding behaviour depend, for their elucidation, on recognition of the amount of food available to the animals. Frequent observations of the presence of 'food' partially consumed or even ignored, at times of low overall feeding activity, suggested that Indri at Analamazoatra, eating the commonest plants of the forest and being physiologically able to remain active for longer periods when required, retained a nutritional credit. The animals were active for only 5 or 6 hours daily for much of the year, approximately half this time being spent feeding, but were all apparently in perfect health. The possibility remains, however, that specific foods, perhaps consumed in small quantities, constituted practical limits for Indri nutrition. Although there were reasons to believe that the adult female of Group V controlled the amount of time spent feeding by the adult male, this was not apparently related to poor levels of food in the forest.

According to the high frequency of local movements, fluctuating feeding activities and the rapid transit through rarely visited areas, it has been suggested that Group V knew little about the location of food in their home range. This view is supported firstly by the belief of the local people that the home range had only recently been adopted by this group, and secondly, by observation of unconsumed food in trees during the period of least feeding activity. The presence of social constraints - relative positions in trees, proximity and activity of group members, and displacements of some individuals by others - on feeding under conditions where there apparently existed a plentiful supply of food, suggests the maintenance of social controls which, despite being presumably concerned with survival in sub-optimal habitats, persist undiminished at other times. When food becomes scarce, the matriarchal society in Indri (and other lemurs) may confer a reproductive advantage to a pregnant or lactating female at the expense of her mate. To determine whether the accentuated form of feeding controls exhibited in Group V by the adult female result from the presence of an infant, low levels of food in the forest or the unacquired intelligence of food location, a further study examining a wider sample of groups is required.

12. SUMMARY

1. Indri are capable of feeding at all levels of the forest. Suspended feeding postures permit Indri to obtain food from the most terminal parts of trees whilst postures used for locomotion are adopted for feeding on young sapling vegetation. Individuals varied in techniques of feeding but food was never picked manually.

2. The proportion of time spent feeding during each Circuit varied more for Group V than Group P across the year. Both groups fed more when the activity period was longest. During the day Indri gradually increased the proportion of time spent feeding to peak at about midday, but for Group V suckling by the infant interrupted this pattern.

3. At least 62 species of plant were eaten by Indri at Analamazoatra. Both groups concentrated equally on the same number of species and these species were generally identical. Thus the diet of the 2 groups was essentially similar. Both groups fed equally on fruit but Group V probably ate more young leaves than Group P. Both groups fed regularly on small amounts of earth.

4. Indri probably eat the commonest plants of the forest but appeared during the study to select some individual trees within species in preference to others. Diversity in diet was assumed both daily and over

several days. Furthermore, the diet changed completely every four months. Indri appeared to organise their daily diet and tended to continue feeding on the species they had previously been eating in a different place.

5. Variation between Circuits in diet and movements to obtain food could be accounted for by the presence of only single sources of food. No seasonally changing trends in diet were apparent.

6. Individuals varied in the amount of time they spent feeding, feeding rate and to a lesser extent the type of food consumed. In general adult males fed the least and fed on more fruit and less shoots than others, throughout the year.

7. The amount of time spent in a quadrat was not significantly correlated with the number of species eaten in that quadrat. Group V tended to spend less time in parts they infrequently visited, moved more within quadrats and changed trees more often than Group P. The proportion of acutely angled turns each group made between quadrats was correlated with the proportion of time spent feeding by Group V but not by Group P. Within Group V the greater the number of angled turns made the less the adult male fed.

8. The proportion of time spent feeding by the adult male of Group V was found to be determined and in all likelihood, controlled by the amount of time he spent

feeding whilst the adult female was simultaneously feeding. This was not true for the adult male of Group P but the presence of some animals clearly if mildly, inhibited or facilitated feeding in other group members.

CHAPTER 7

Ranging Behaviour

1. INTRODUCTION

In this chapter the position and changes of position of groups in their ranging area are considered and the function of these movements examined. Three aspects of ranging behaviour are distinguished: the amount of time spent in different parts (home range utilisation), the movement between different parts (ranging behaviour), and the small or 'local' movements made as Indri move to different parts of the home range (local movements).

Three questions dominate the analysis of data in this study of Indri ranging behaviour:

(1) In what ways is Indri ranging behaviour affected by external influences such as weather, season, or the presence of other groups in certain parts of their own ranges?

(2) Do Indri move in predictable patterns around the home range and, if so, is this related to obtaining the correct food?

(e) Can differences in the way groups use and move about their home ranges be explained by differences in the home ranges (e.g. food distribution and abundance) or by differences in some properties of the groups themselves (e.g. knowledge of food location)? For example, spending less time in certain parts of the home range could result either from (1) visiting those parts less frequently than others, or, by (2) spending less time in them than in others on every visit. Evidence for strategy (1) above might be suggestive of animals being aware of a dearth of food in these parts and for strategy (2) of being ignorant of this fact.

When an Indri group moves about its range, individuals behave as a cohesive unit rapidly following one after the other during long progressions. Except in rare instances when animals become temporarily dissociated from the rest of a group, the members of a group move in the same direction at approximately the same time.

The issue of Indri territoriality - see Chapter 9 - is again avoided in the following discussion as it does not appear to be central to the specie's ranging behaviour.

2. LOCOMOTION

2.1. Movement and vertical clinging and leaping.

Large 'vertical clinging and leaping' (Napier & Walker 1967) lemurs such as Propithecus and Indri move underneath or in the lower parts of the canopy, engaging in short sequences of leaps - usually from one vertical support to another. Each sequence is composed of 2-8 leaps and carries the animal a total distance of between 10 and 30 metres. Although single leaps can be as long as 10 metres, Indri normally choose easy pathways involving successive sequences of 3 to 5 leaps - each of horizontal distance about 3 metres.

The mechanics of Indri locomotion has been already described in detail by Walker (1967). Vertical clingers and leapers are characterised by low intermembral indices[1].

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[1] The intermembral index is: $\frac{\text{(Humerus+Radius length)}\times 100}{\text{Femur+Tibia length}}$

For Indri the index is 64 (n=13, Napier & Napier 1967) and lies at the upper limit for vertical clinging and leaping forms (Walker 1974). The intermembral index for a specialised brachiater such as the gibbon is 129 (n=66, Napier & Napier 1967). Unlike other prosimian species that move in this way, Indri and Propithecus commonly use as their vertical supports the trunks of the largest trees in the forests. The canopies of such trees are often dense and wide and very little vegetation grows underneath them, allowing the animals an unobstructed medium in which to move very rapidly.

The sequence of movements executed by leaping Indri are shown by typical body positions in a series of plates in Plate 7.1. Resting postures apparently use frictional properties of the foot against the tree as the main vertical supporting force (see Cartmill 1974). The feet are spread around the trunk rather than grasp it. In this way trunks as great in diameter as 100 cms may be used as supports for vertical clinging and leaping locomotion. The arms are used solely to keep the body close to the trunk of the tree so that the centre of gravity of the animal passes vertically through its body and acts at the minimal horizontal distance from the supporting force.

An Indri in this position prepares for a leap by swivelling the head 180° in the direction of the proposed movement . Vertical clinging and leaping primates take off backwards and thus require exceptional mobility in the axis-atlas and other cervical articulations. Having

PLATE 7.1 Vertical clinging and leaping locomotion (VCL) in *Indri*. Plates a-d represent successive stages in a single leap (see text).

(a)

(b)

PLATE 7.1 (continued)

(c)

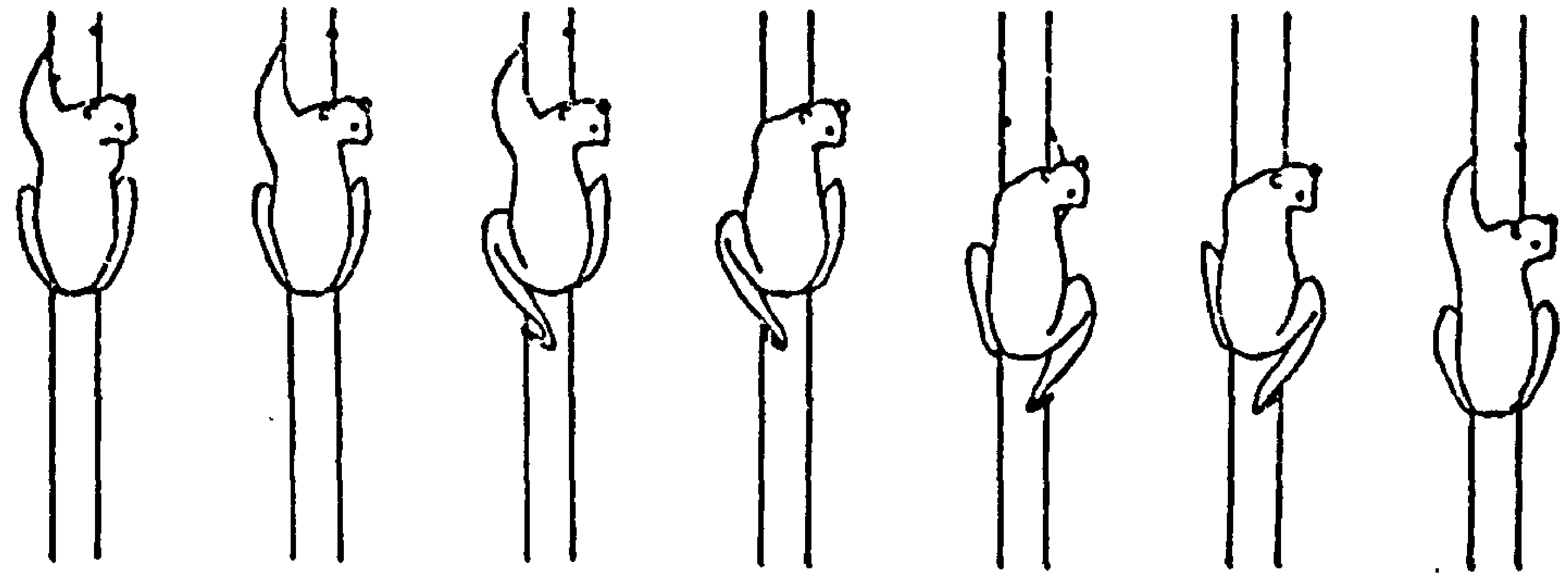
(d)

visually selected the landing support, the upper body is allowed to fall from the tree trunk by relaxing the arm hold. As this happens the upper body swivels to the side (Plate 7.1a). It may not be until the angle of the body is about 30^{o} from horizontal that the hind limbs push powerfully off the trunk. The legs are brought forwards early in flight and the animal, whose arms are normally held high, takes on a crouching posture (Plate 7.1 b-c). The head points towards the landing support from before take-off and the upper body and legs successively turn into this attitude. During long leaps the body planes by adopting a gliding attitude, the arms pulling laterally the broad expanse of skin (Milne-Edwards & Grandidier 1875) that stretches from the side of the chest to the upper arm and which may act as a flying membrane to a limited extent. First contact with the landing support is usually made by the legs which are brought forward towards the end of the leap. Often, however, arm and leg contact occur either simultaneously (Plate 7.1c-d)or even arms first. The momentum of the body flexes the hind limbs into a posture ready for another leap, and, if landing occurs at a tangent to the trunk, causes the body to swing around it into a position from which the direction of travel can be maintained . Supports taken in the middle of a leaping sequence are usually momentary. A full 'clinging' (Plate 5.4) posture is often not achieved and the animal may land, swing partly around the tree-trunk, and push off again using only the fore and hind limb of one side of the body. In these cases, the trunks do not fully obstruct the direction of travel and the animal tends to move either in wide arcs (by using the same side of successive trees) or in straight lines (by using alternate sides of successive trees).

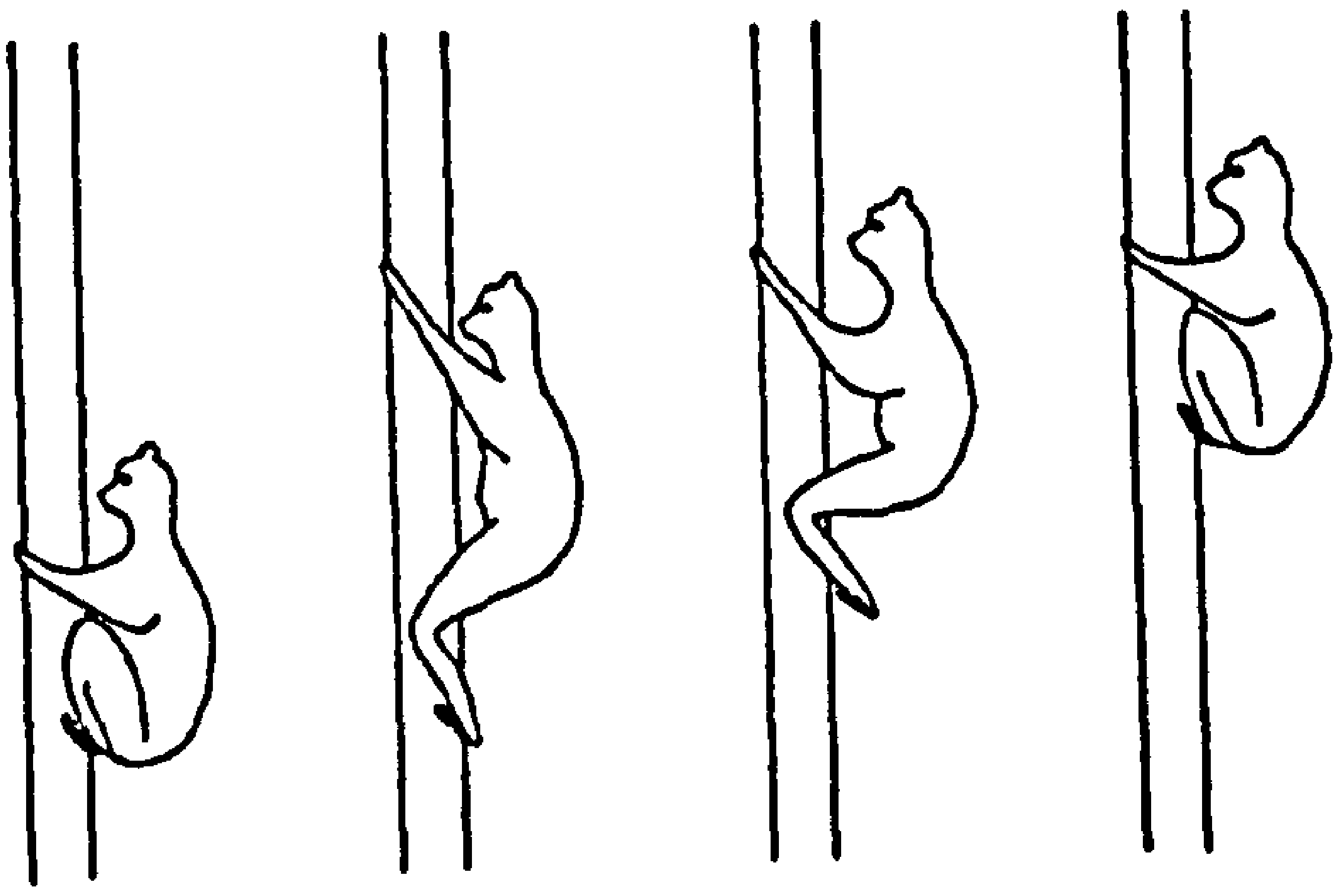
Habituated Indri at Analamazoatra moved in the way described above, ascending to feeding positions by grasping the tree-trunk with both arms and making two-legged vertical hops. (Figure 7.1). Descent from large trees would be accomplished by 'walking' down the trunk backwards, using each fore and hind limb alternately (Figure 7.1).

The power of the hind limbs is exceptional. From the ground Indri are capable of jumping vertically upwards at least 8 feet, and are thus able to perform about 200 foot pounds of work in less than a second (equivalent to at least one third of a horse-power). Leaps were not parabolic in passage as suggested by Charles-Dominique & Hladik (1971) for Lepilemur mustelinus, and height relative to the starting position was more often lost than gained. Indri were not observed to often take the trajectory mathematically best suited for maximum distance (i.e. leaping at an angle of 45^{o}) as to achieve a great distance was not the objective for most leaps. Studies of the ontogeny of the leaping ability (see Chapter 10) indicated that landing is the most difficult skill to acquire, and is seen to cause most locomotor problems for Indri. Thus Indri tend to leap well within their capability as far as distance is concerned, the body attitude and velocity at

Figure 7.1 Cartoons of *Indri* movement. Descent and ascent of vertical tree trunks.



Descent



Ascent

landing being of prime importance and affecting the angle, speed and direction of take-off.

On the ground Indri do not stagger bipedally or make two-footed hops with raised arms like Propithecus. Their arms are held low and the body is crouched, exploding into one or two forward leaps from this position in order to reach the nearest tree.

In the primary vegetation at Fierenana unhabituated Indri commonly fled from the observer at the level of 'canopy bottom', using large angled boughs to maintain heights of 30-40 metres above the ground. It was not possible to ascertain if these supports were chosen to keep further away from the observer or if the greater stature of trees in this study area made VCL locomotion more difficult. The former interpretation is preferred, however, as occasionally Indri were stalked to a position from which they could be seen whilst they were unaware of the observer, and in these cases moved lower in the forest.

The lack of a tail seems to have no effect on Indri locomotion compared with that of the tailed sympatric indriid Propithecus diadema diadema. The tail of Tarsius is apparently essential for providing support in VCL resting postures (Grand & Lorenz 1968), but Indri can remain on a vertical trunk with no pelvic support for indefinite periods and Propithecus spp. let their tail hang limply in the same postures. Some VCL prosimians apparently use the tail as a steering mechanism during flight (Charles-Dominique 1971). The tail was not obviously important as a steering device in Propithecus locomotion and Indri did not appear to be in any way limited in the control of direction during leaps. For large bodied VCL primates living in very dense vegetation a tail may restrict rather than facilitate movement.

On the basis of observations made during this study, five species of lemur in the study areas can be classified as 'vertical clingers and leapers' (Table 7.1). These include Hapalemur griseus and Lepilemur mustelinus as well as the three indriids (Indri, Avahi and Propithecus), and the locomotor classification of Napier & Napier (1967) is thus preferred to that of Walker (1974). Hapalemur, however, live mostly under the canopy of large trees, occupying the dense vegetational milieu of bamboo thickets and secondary growth, and therefore use supports of small diameter. In addition, Hapalemur is less specialised in choice of support than other VCL lemurs, often jumping to land on angled or even horizontal stems rather than vertical ones.

2.2. The structure of the environment and Indri locomotion.

Two obvious effects of the topography and vegetational structure of the montane rain forest on lemur movements were recognised during the course of the study:

(i) The dense undergrowth lying about some parts of the forest - especially near ridge-tops - put a high premium on arboreality for large mammals, including the endemic carnivorous viverrids (Albignac 1973). The two major locomotor systems adopted by large bodied Malagasy

Species	Activity	Locomotion	Vertical Position	Height of travel	Environment
Microcebus	Nocturnal	Small VCL + quadrupedal	All heights (Fine branch niche)	ALL	Foliage at all levels
Cheirogaleus	Nocturnal	Small VCL + quadrupedal	?	?	Foliage
Lepilemur	Nocturnal	VCL	?	?	?
Hapalemur	Crepuscular	VCL	Under canopy	<20 ms	Bamboo thickets secondary veg. small tree canopies
Lemur Fulvus	Diurnal + nocturnal	Quadrupedal	ALL CANOPIES	10-40 ms	Foliage of all large trees
Varecia variegata	Diurnal + ?	Quadrupedal + liane climber	Highest canopies (only?)	<40 ms	Tree tops
Indri	Diurnal	VCL	All parts except canopy tops	5-30 ms	Trunks at all heights. Canopy bottom
Propithecus diadema	Diurnal	VCL	?	?	?
Avahi laniger	Nocturnal	VCL	?	<20 ms	?

TABLE 7.1. Locomotor types in Rain Forest living lemurs.

lemurs - 'vertical clinging and leaping' in sub-canopy or thicket environments (e.g. Indri), and, quadrupedal movement across canopy platforms (e.g. Lemur sp.), have slightly different consequences for food attainment capabilities. It was not evident that some foods, by their position in the forest, were unobtainable by large VCL primates such as Indri. Lemurs unable to VCL on trunks of wide diameter, however, were denied access to two sorts of trees:

(a) Trees whose canopies were separated from those of adjacent trees horizontally, and,

(b) Trees whose canopies were separated from those of adjacent trees vertically.

Instances of (a) above, were commonly observed in partially degraded forests such as Analamazoatra or after natural tree fall in primary forests such as Fierenana. Instances of (b) above, occurred in all forests with emergent vegetation.

(ii) The montane structure of the majority of the eastern forests in Madagascar is acute, slopes at ridge-tops often attaining angles of 30°-40° (Plate 2.2). Although the trees at valley bottoms are higher than those at ridge tops, which to some extent buffers the gradient that lemurs move on, different techniques may be required, for moving up and down the slopes. Moving downhill, for example, is easily accomplished for both platform using and vertical trunk using lemurs. Moving uphill, the animal is faced by a different (lower) part of the tree in which to move into. *Indri* reduces height relative to the ground at each leap (being unable to leap upwards very far) and therefore has to stop from time to time in order to regain height. *Lemur fulvus*, however, running along the canopy is able to move continuously by taking canopy bottom to canopy top pathways within each tree.

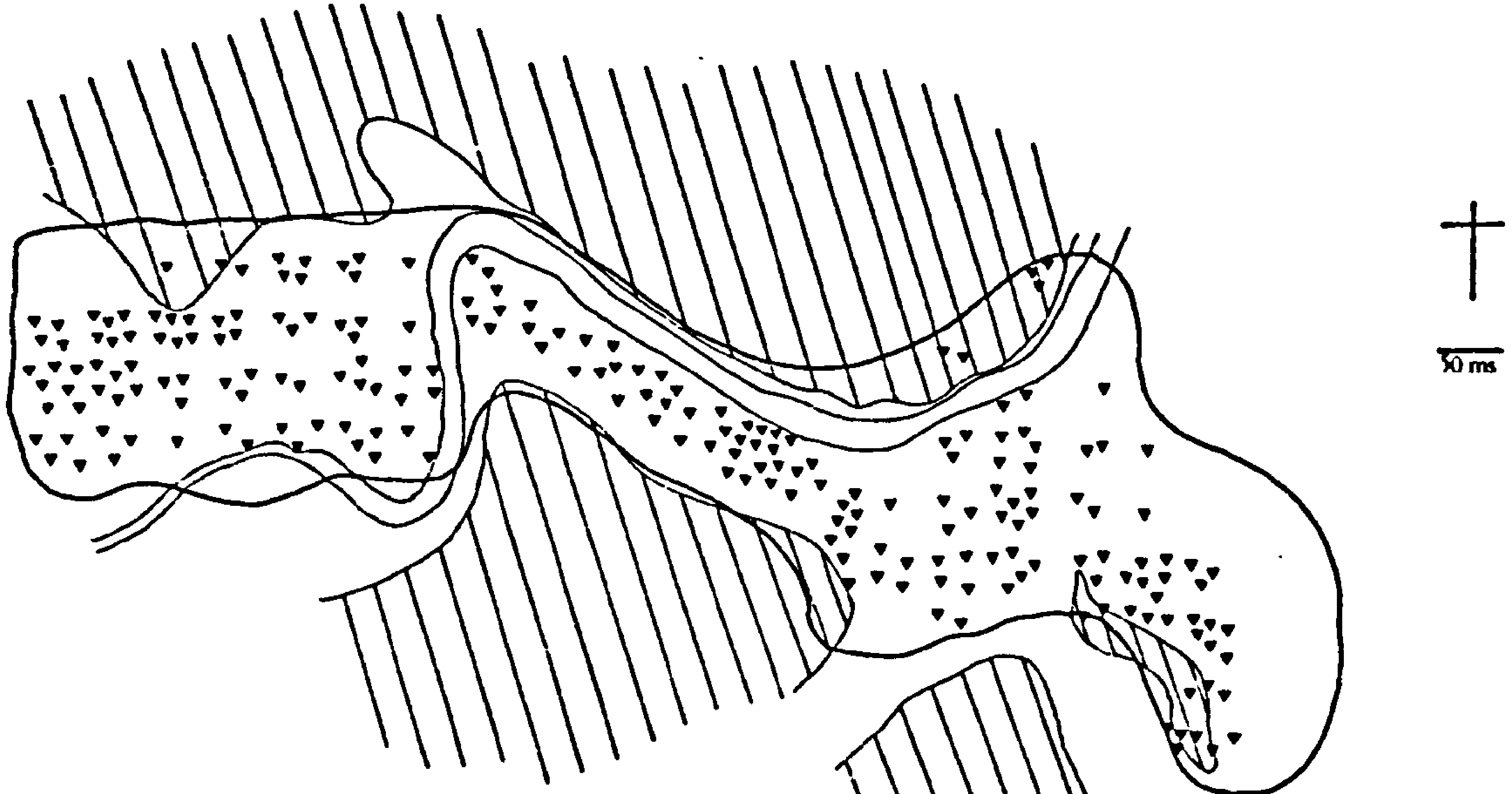
One may speculate that a canopy bottom brachiator such as *Hylobates* would experience difficulty in moving up such a slope, unless the ability to brachiate and gain height is well developed, and in moving down the slope as the canopy of the next tree would obstruct the best supports required by the animal.

3. HOME RANGE UTILISATION BY INDRI

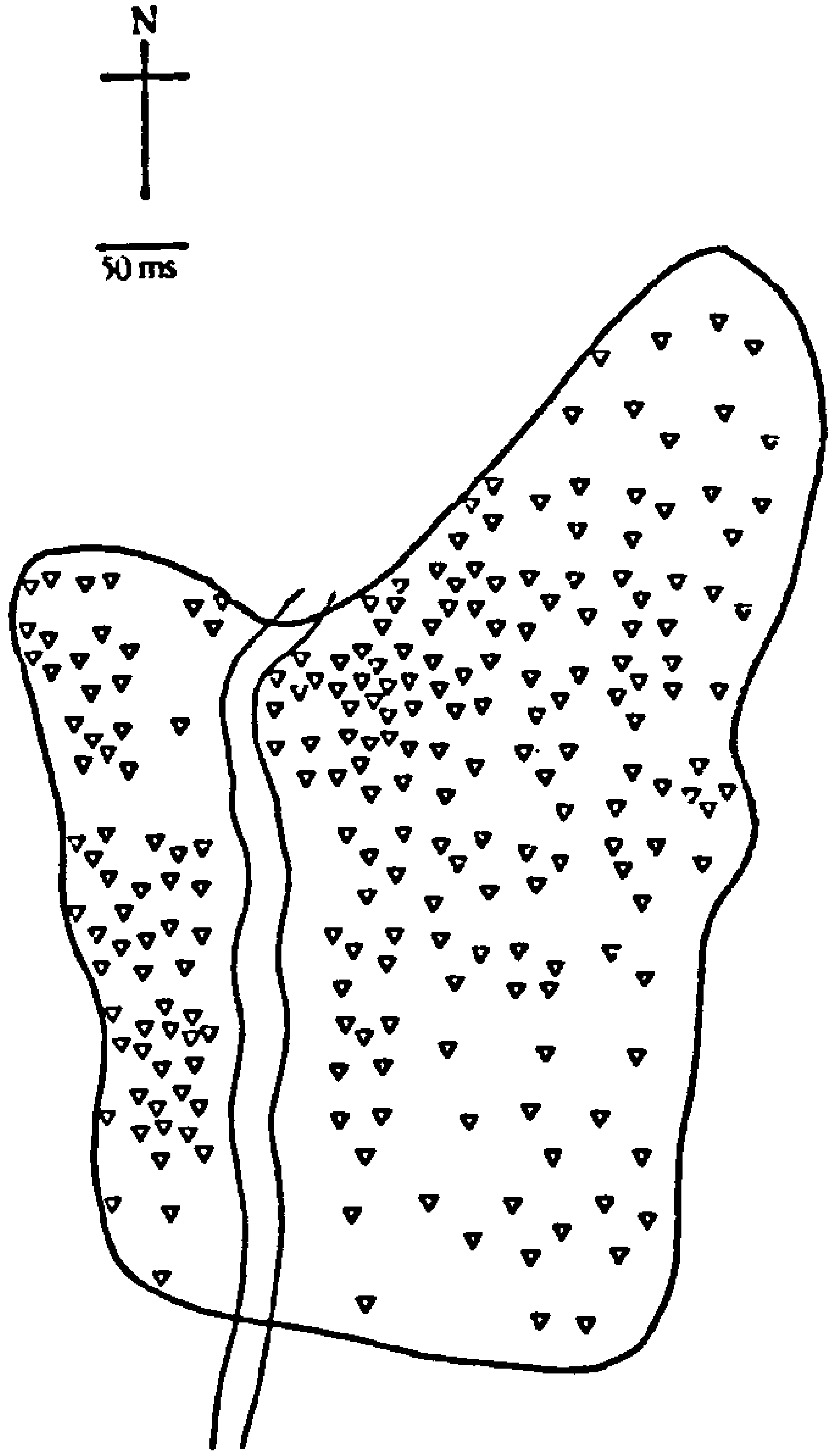
Gross measures of home range utilisation for Groups P and V are shown in Fig. 7.2, where 30 minutes spent in a 50-metre sided quadrat over the whole year is illustrated by one point. Over the year all parts of the area enclosed by the ranging limits were visited, although regions bordering the territories (see Chapter 9) of adjacent groups were less frequented than others.

At any one time, *Indri* at Analamazoatra used some parts of their home range more than others. Some quadrats were frequently entered throughout the year and these gave an overall skewed appearance to the distribution of time spent in all quadrats (Fig. 7.3). Only quadrats in which at least 1.5% of the time was spent are illustrated in Fig. 7.3, and these consist of 30 quadrats (42.8% of the total ranging area) and 32 quadrats (45.8% of the total

Figure 7.2 Home range utilisation in Group P and Group V. Each spot represents 30 minutes of time spent in part of the home range throughout the year. Each spot is no more accurately localised than the quadrat (50 metre-sided) containing it and does not, therefore, represent point localisation.

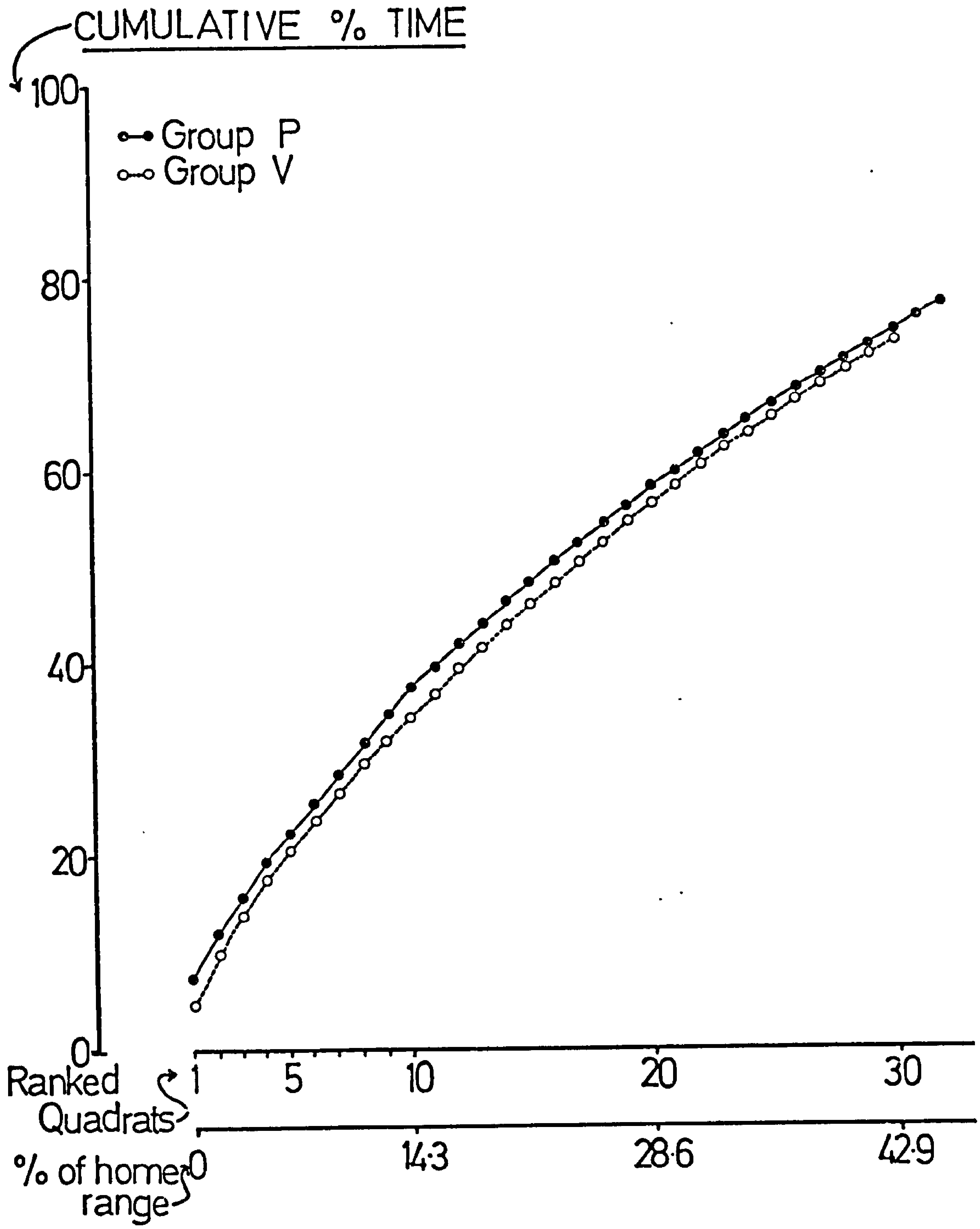


Group V



Group P

Figure 7.3 Quadrat selection in Group P and Group V. The cumulative percentage of time spent in the most used quadrats over the year in each group are illustrated. Only quadrats in which at least 1.5 % of the time was spent are shown.


CUMULATIVE % TIME
100
80
60
40
20
0
Group P
Group V
Ranked Quadrats
1
5
10
20
30
% of home range
0
14·3
28·6
42·9

ranging area) for Group P and Group V respectively. The cumulative percentage of time spent in these quadrats was 77.3% for Group P and 73.3% for Group V. Group P spent 50% of its time in 25.7% of its home range and 30% of its time in 11.4% of its home range. Corresponding figures for Group V are 22.2% and 11.1%.

Seasonal variation in activity period was great. During the summer (wet) season the length of the activity period increased over the winter mean by 59.1% for Group P and 51.1% for Group V. Measures of the percentage of total time spent in a given quadrat over the year, therefore, weight against winter observation periods, and the most ecologically appropriate consideration - the percentage of mean time spent in each quadrat in each Circuit - is ignored. The average amount of time spent in a quadrat each Circuit over the year was therefore computed and compared with the total time spent in each quadrat. The two results were found to be very comparable and when ranked against each other (non-parametric tests being used), only one change in rank order position was noted - one of the heavily used quadrats shifting one position. Overall measures of time spent in a quadrat were considered, therefore, to be representative of the concentration of each group on certain quadrats according to the differing amounts of time available to them each Circuit.

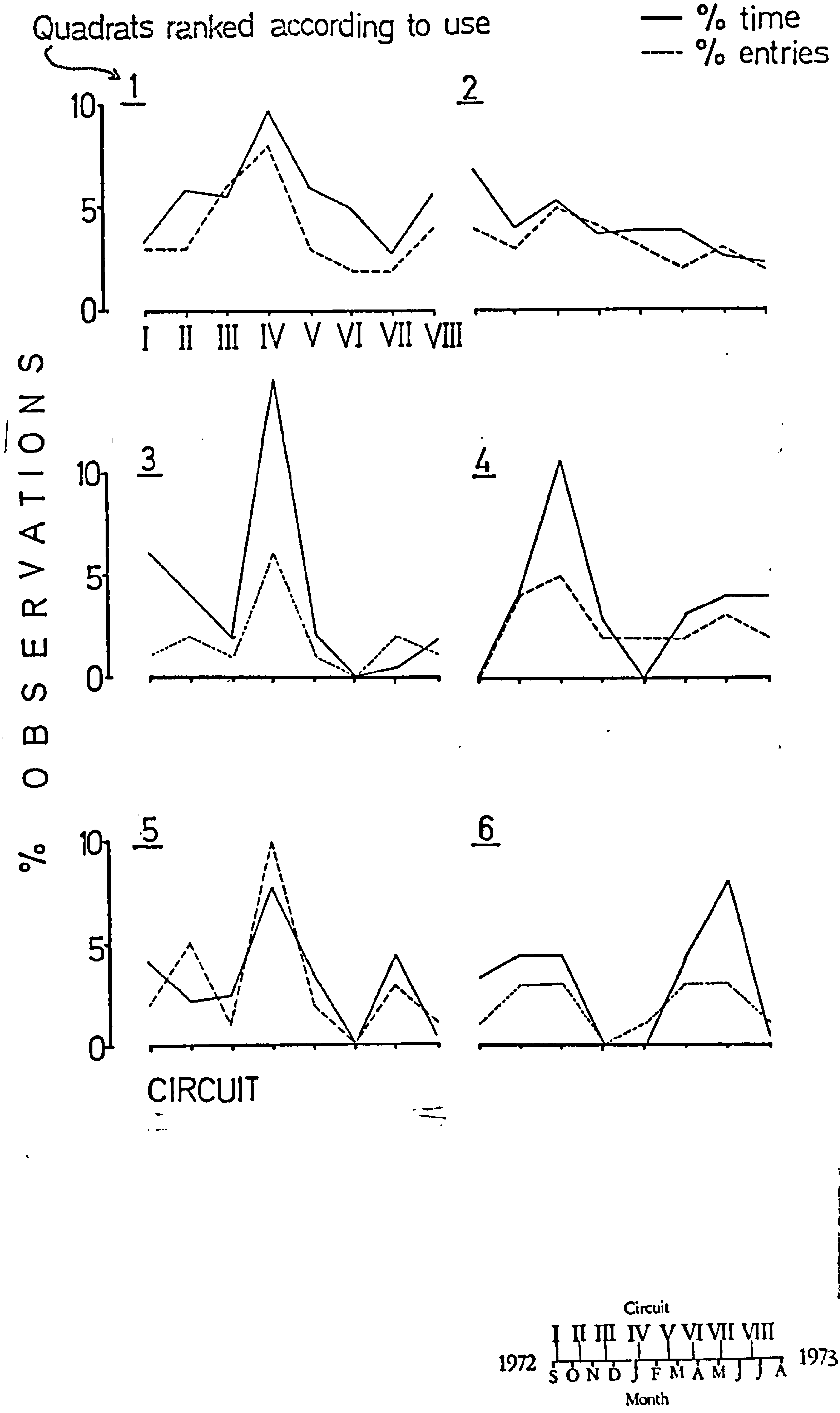
To investigate whether some quadrats were more evenly used over the year than others, seasonal variation in the amount of time spent in the top ten ranking quadrats (ranked according to the overall amount of time they were occupied) was considered (Fig. 7.4 a-b). For Group P only 2 quadrats were used in every Circuit and only one of these was used approximately evenly throughout the year. No quadrat in Group V was used during every Circuit. Considerable peaks were shown in the amount of time spent in high-ranking quadrats at certain times of the year by Group P. Five Circuits in this Group contained observations in which one quadrat peaked in this fashion. In Circuit IV there were 3 such quadrats, in Circuits V there were 2 and in Circuit VI there were none. For most of the year, therefore, only one quadrat was visited much more than the others, whereas in the summer a greater number of these selected quadrats was chosen. In Group V similar peaks occurred in Circuits III (1 quadrat), IV (2 quadrats), V (1 quadrat), VI (3 quadrats), VII (1 quadrat) and VIII (2 quadrats), possibly indicating a less regular seasonal concentration in specific areas.

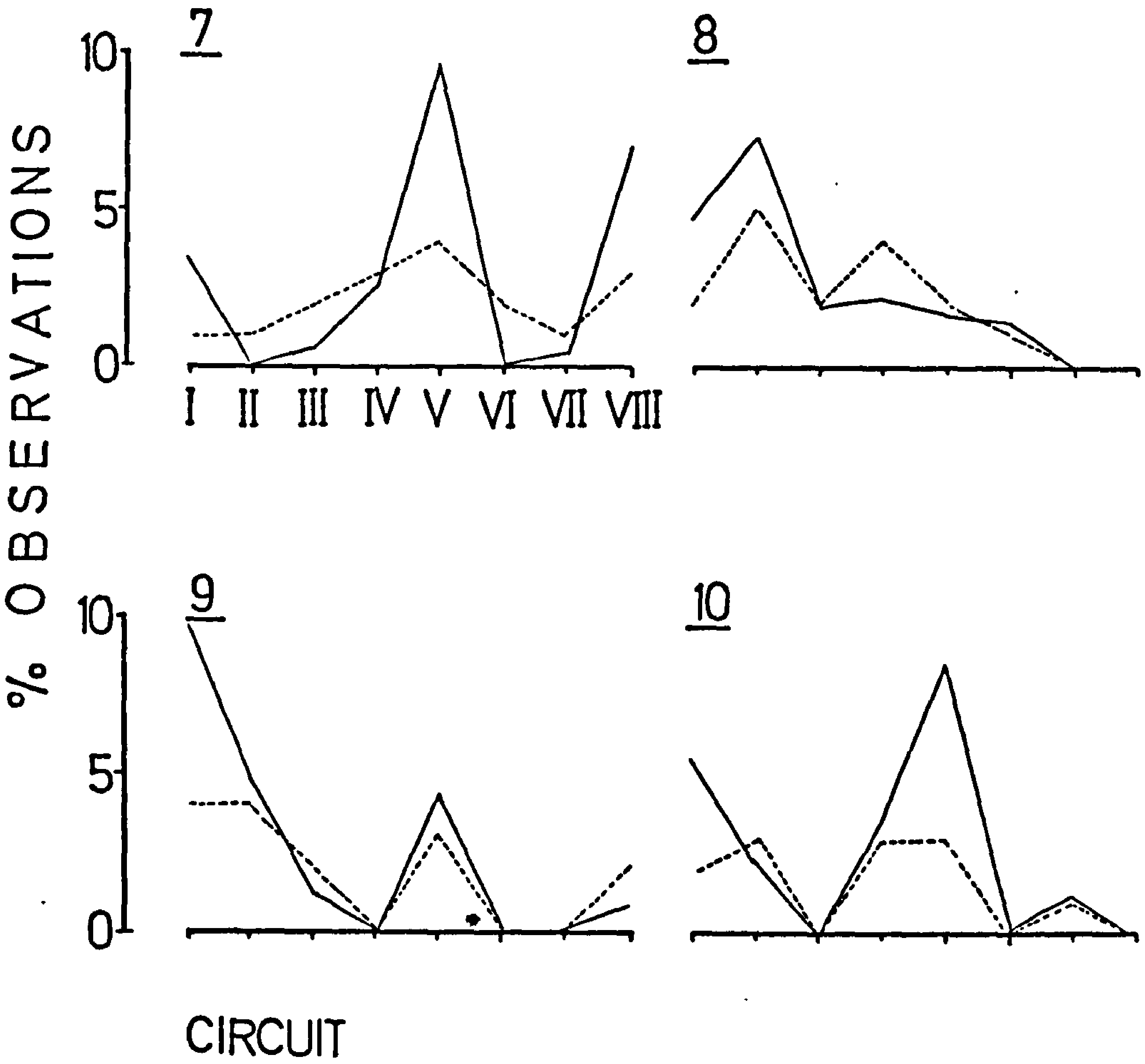
Measures of the percentage time in each Circuit that top-ranking quadrats were used, show a close agreement with measures of quadrat entry frequency (Fig. 7.5). The time spent by Group P in any quadrat each time it was entered was fairly constant and similar throughout the year. This suggests that:

(i) seasonal differences in home range utilisation ensured that even where concentrated food sources were repeatedly and heavily used (perhaps daily), considerable movements about the home range still occurred. This can

Figure 7.4a Seasonal variation in home-range utilisation in Group P. Seasonal variation in the proportion of time spent in the ten most used quadrats over the year and the proportion of entries to each of these quadrats are illustrated.

GROUP P


Quadrats ranked according to use
% time
% entries
1
2
3
4
5
6
10
5
0
I
II
III
IV
V
VI
VII
VIII
% OBSERVATIONS
CIRCUIT
Circuit
I II III IV V VI VII VIII
1972
S O N D J F M A M J J A
1973
Month


% OBSERVATIONS
7
8
9
10
10
5
0
10
5
0
I
II
III
IV
V
VI
VII
VIII
CIRCUIT

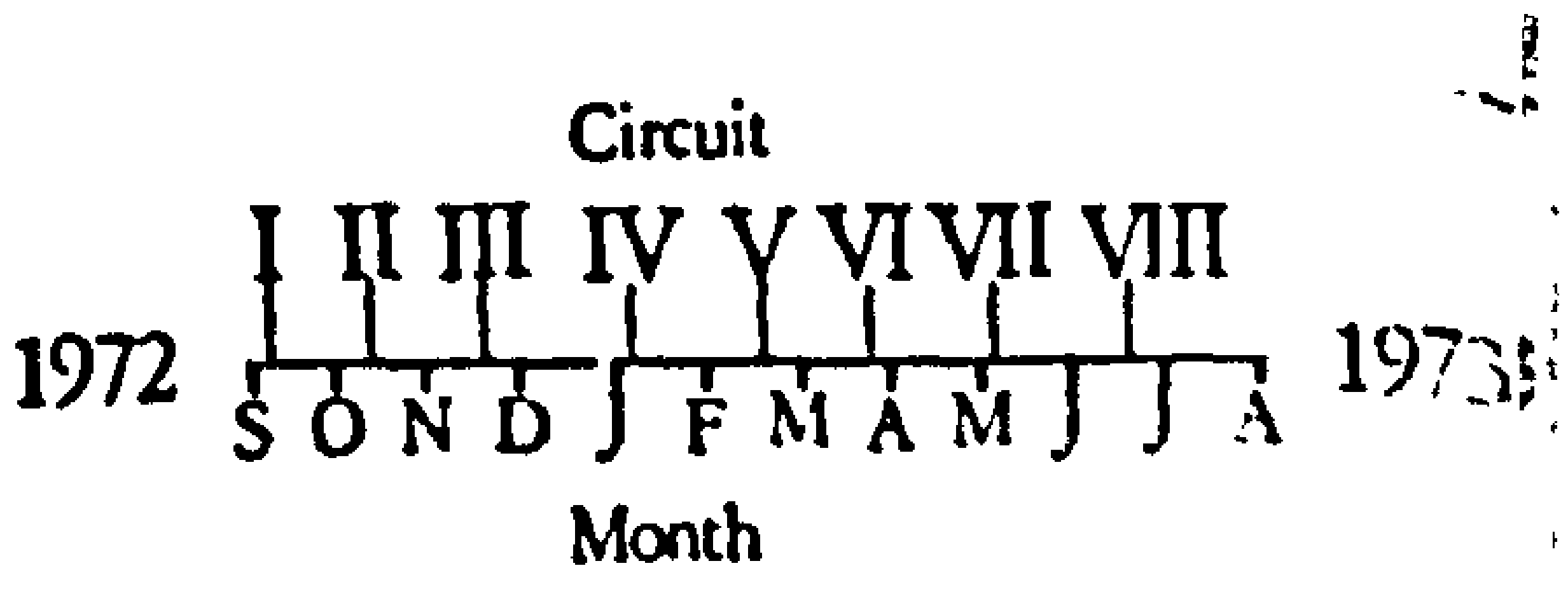
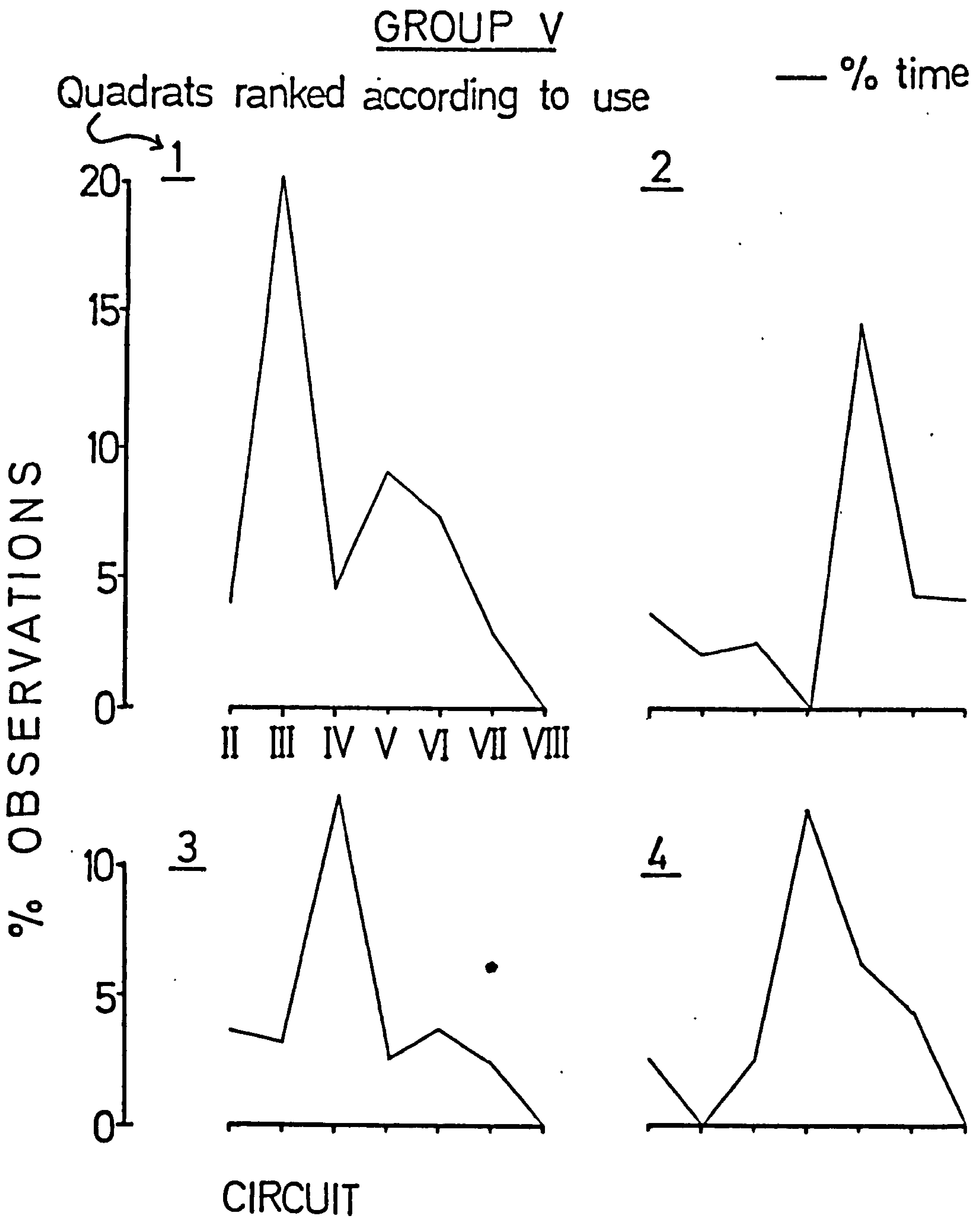
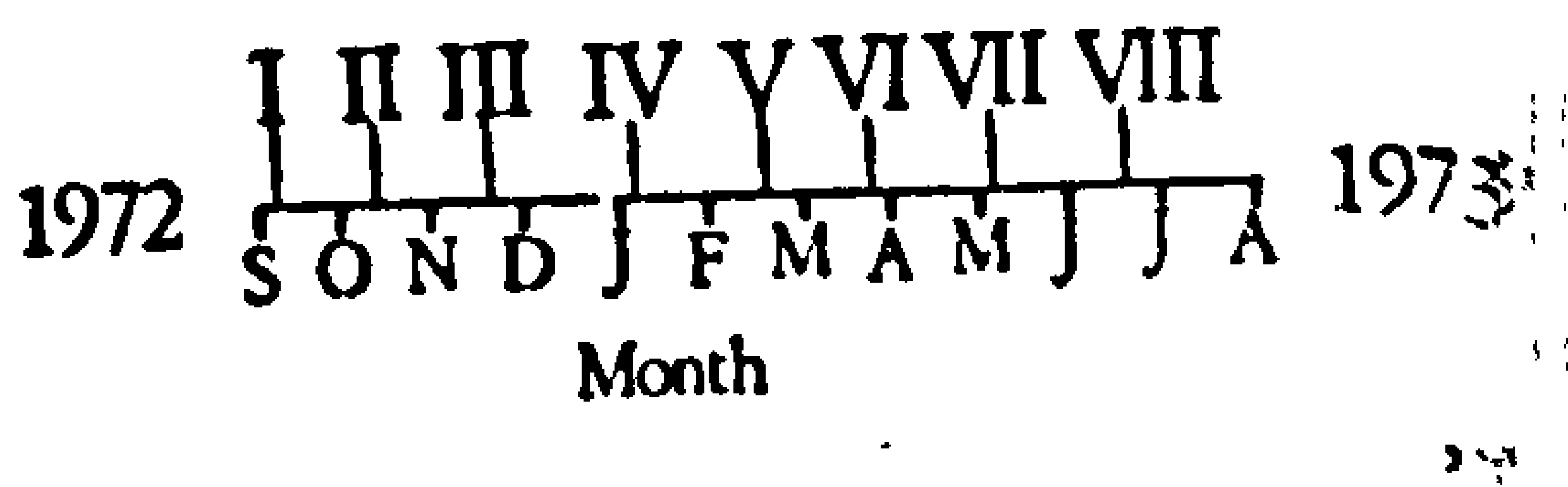

Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
1973
Month

Figure 7.4b Seasonal variation in home-range utilisation in Group V. Seasonal variation in the proportion of time spent in the ten most used quadrats over the year is illustrated.


GROUP V
Quadrats ranked according to use
— % time
% OBSERVATIONS
1
2
3
4
0
5
10
15
20
II
III
IV
V
VI
VII
VIII
CIRCUIT


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S O N D J F M A M J J A
1973
Month

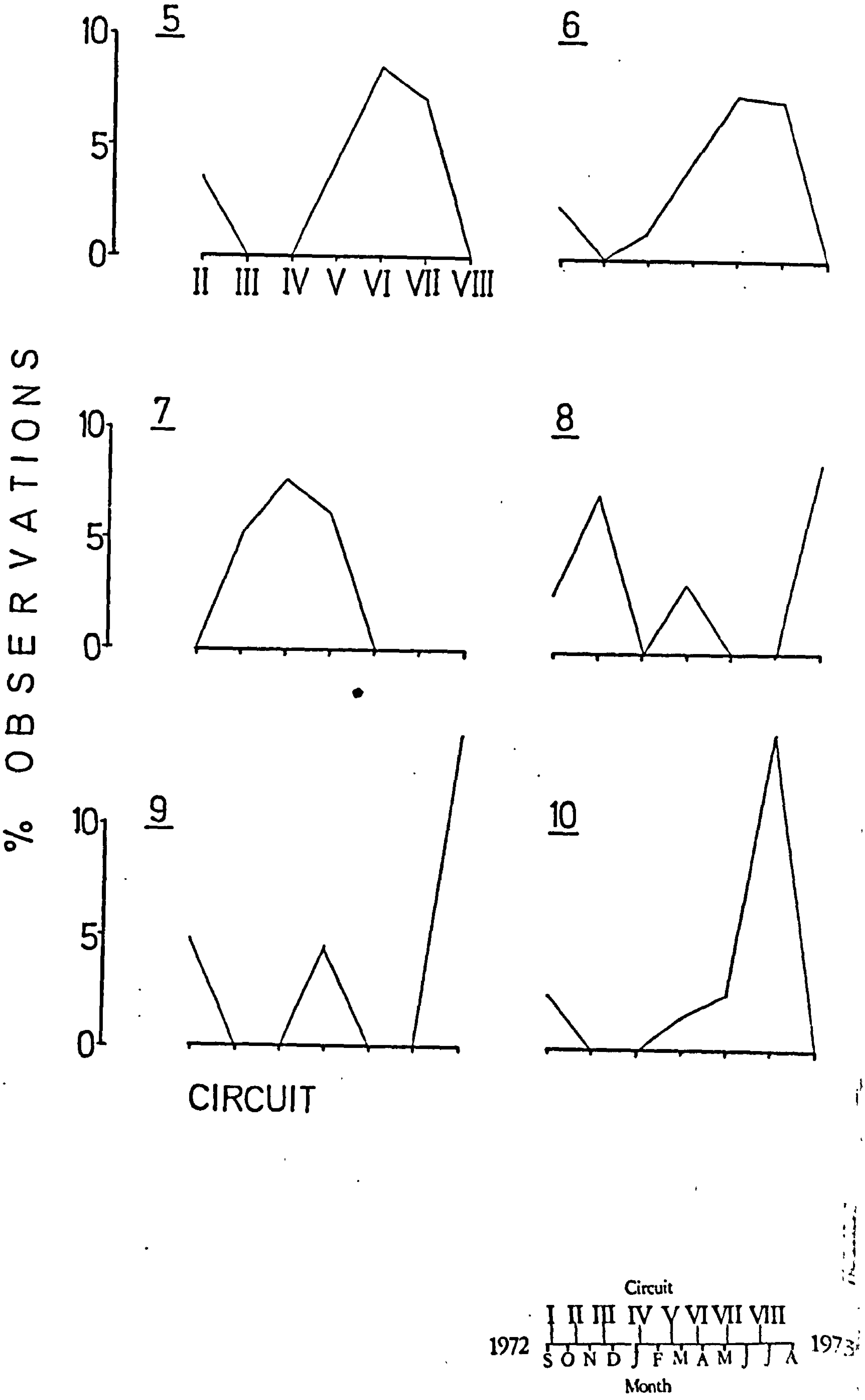
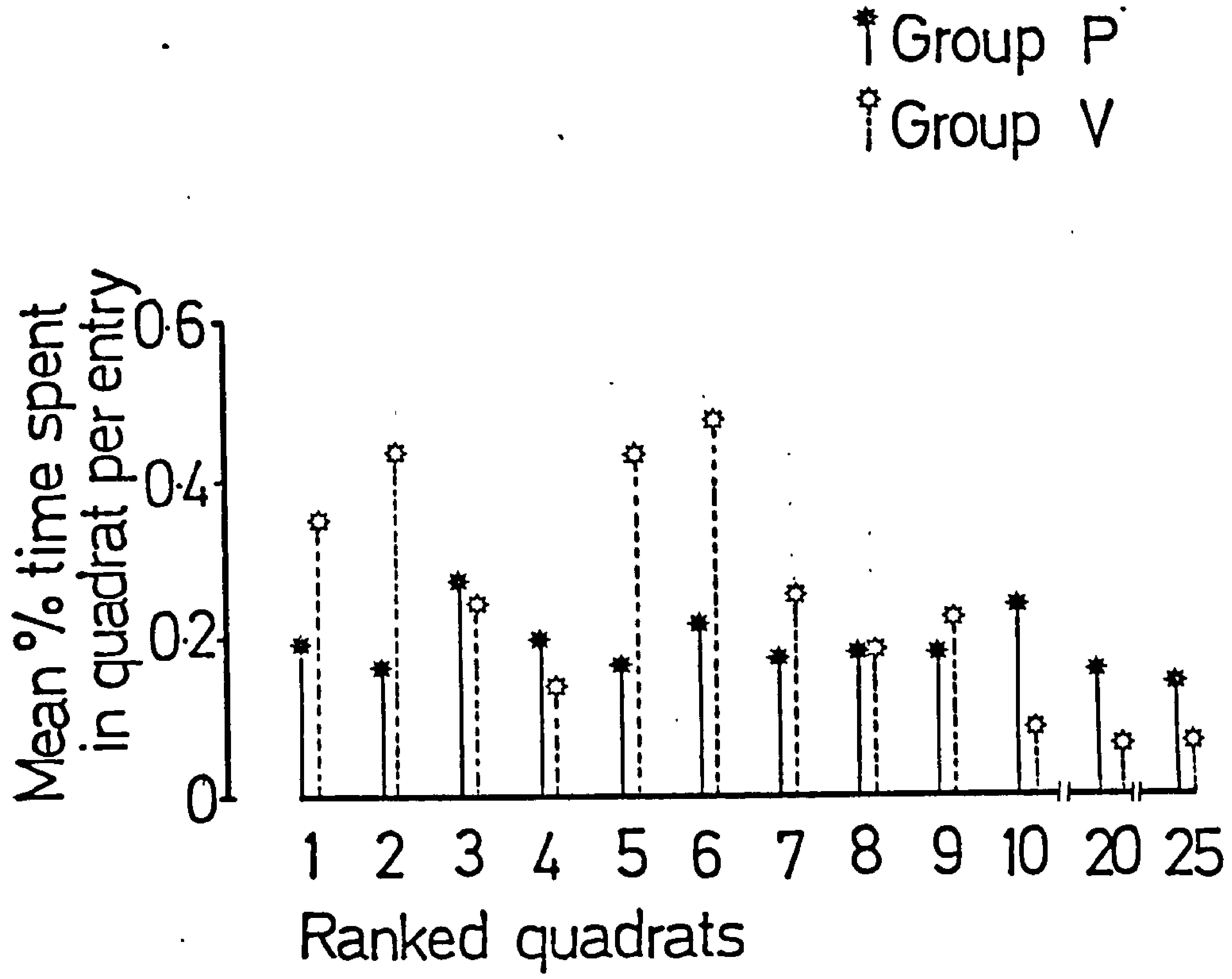
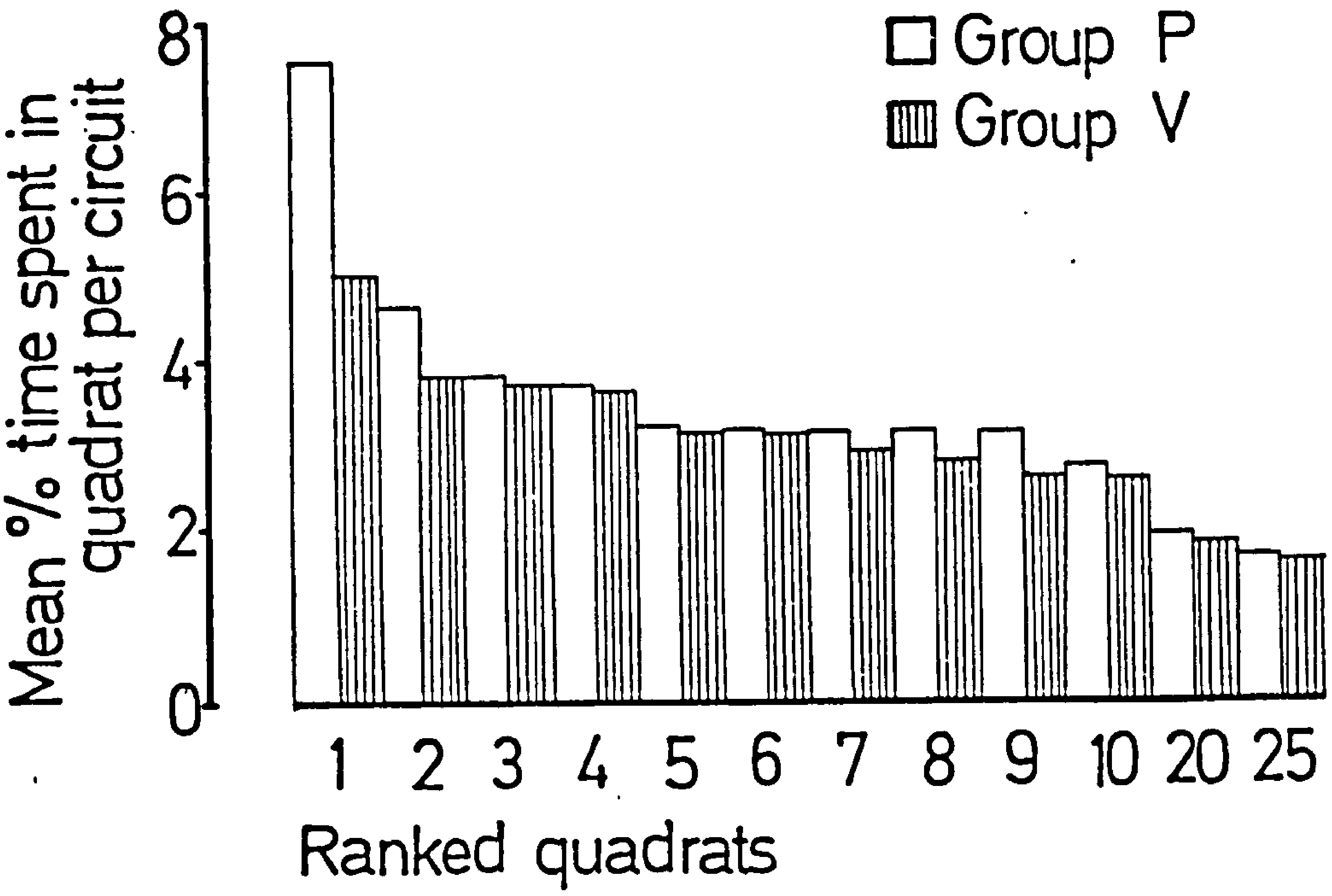

% OBSERVATIONS
10
5
0
5
6
7
8
9
10
II
III
IV
V
VI
VII
VIII
CIRCUIT
Circuit
I II III IV V VI VII VIII
1972
1973
S O N D J F M A M J J A
Month

Figure 7.5 The amount of time spent in quadrats each time they were entered by Group P and Group V. The average time spent in a quadrat each time it is entered is related to the overall amount of time spent in that quadrat over the year (quadrat rank) for both study groups at Analamazoatra.


Group P
Group V
Mean % time spent in quadrat per entry
0·6
0·4
0·2
0
1
2
3
4
5
6
7
8
9
10
20
25
Ranked quadrats


Group P
Group V
Mean % time spent in quadrat per circuit
8
6
4
2
0
1
2
3
4
5
6
7
8
9
10
20
25
Ranked quadrats

be visually appreciated in the ranging maps presented in Section 6 .

(ii) Notwithstanding differences in the frequency with which quadrats were entered, the period of time that they were occupied following each entry was essentially similar. To examine whether Group P visited heavily used quadrats specifically to engage in feeding activities and visited less used quadrats for other reasons, the proportion of time spent feeding in each class of quadrats was computed. The percentage of time spent feeding in rarely visited quadrats was 51.1% and in frequently visited quadrats 47.5%. These did not differ significantly ($X^2_{1df} = 0.677$, $0.5 < p < 0.7$).

Group P, therefore, varied their use of the territory by entering regions with different frequencies rather than spending different amounts of time there once they were entered. They also engaged in feeding activities equally in different parts. *Indri* of this group did make long progressions in which many quadrats were crossed in a few minutes. Over the whole year, however, despite the presence of preferred arboreal pathways, the small amounts of time spent in those parts of the home range visited often in transit, were balanced by longer, feeding visits on other occasions.

Group V appeared to use low ranking quadrats differently from high ranking ones (Figure 7.5). Despite equal dispositions in the two groups to spend most time in some parts of their home ranges (Fig. 7.3), the mean time spent in a quadrat per entry decreased with quadrat rank in Group V whilst remaining stationary in Group P.

It is unlikely that food distributions varied enough between the 2 adjacent home ranges to account for this difference, and the geometry of the Group V home range did not influence this result, as quadrats which had to be visited in order to reach other areas were not those in which least time was spent.

For Group V the activities performed in the 2 quadrats in which most time was spent (total 12.0% of the time) were compared with the activities performed in the 11 quadrats in which least time was spent (total 5.5% of the time). As in Group P, this group fed equally in high and low ranking quadrats ($X^2_{1df} = 0.183$, $0.5<p<0.7$).

4. SLEEPING LOCATIONS

Indri sleep at the lower levels or underneath the canopy of any large trees with satisfactory supports. They balance themselves on a small, horizontal branch junction, or support themselves on a wide, horizontal bough (Plates 7.2,3.1).Although sleeping trees appeared to be abundant, a short final progression was sometimes executed to take them to a tree they had slept in previously. Under these conditions individual animals would repeatedly adopt the same positions and postures. It could not be established with certainty whether or not these final progressions were made in order to sleep at a specific site because they were normally interrupted

PLATE 7.2 Typical 'canopy bottom' sleeping posture in *Indri* (Group P adult female).

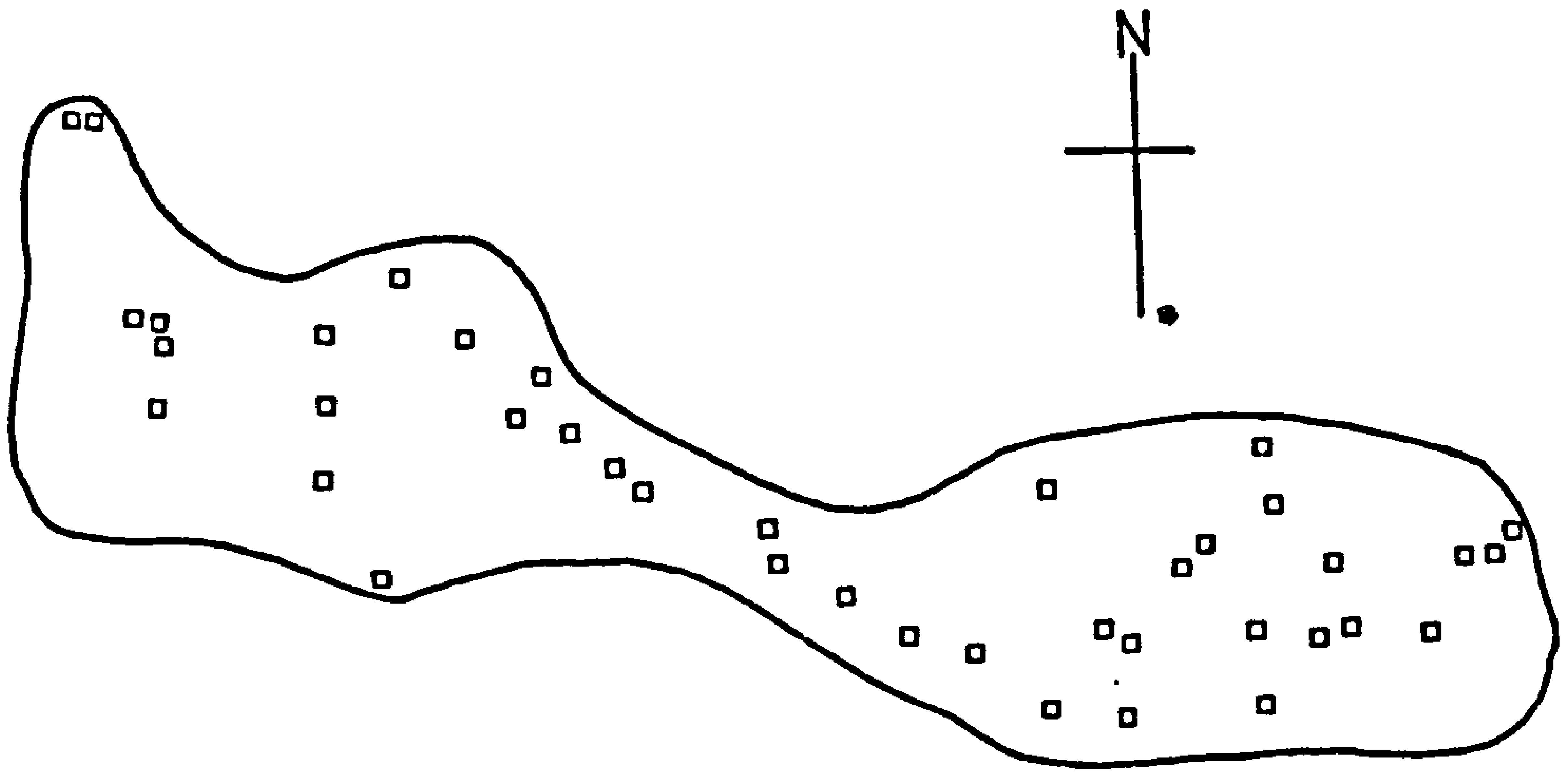
with short feeding bouts. Animals often simply took sleeping positions in a feeding tree by moving a few metres to a more structurally stable location.

Indri sleep in all parts of their home range (Figure 7.6). The places most often slept in were apparently the places in which most time was spent overall for Group P, although insufficient data were collected to confirm this statistically. The most used quadrat was most often slept in, but the second most used quadrat was never slept in. This was probably because during Circuit IV Group P repeatedly fed in one part of the home range and slept in another (see Section 6). Occasionally, the group would be dispersed across quadrats, making records of sleeping location inaccurate.

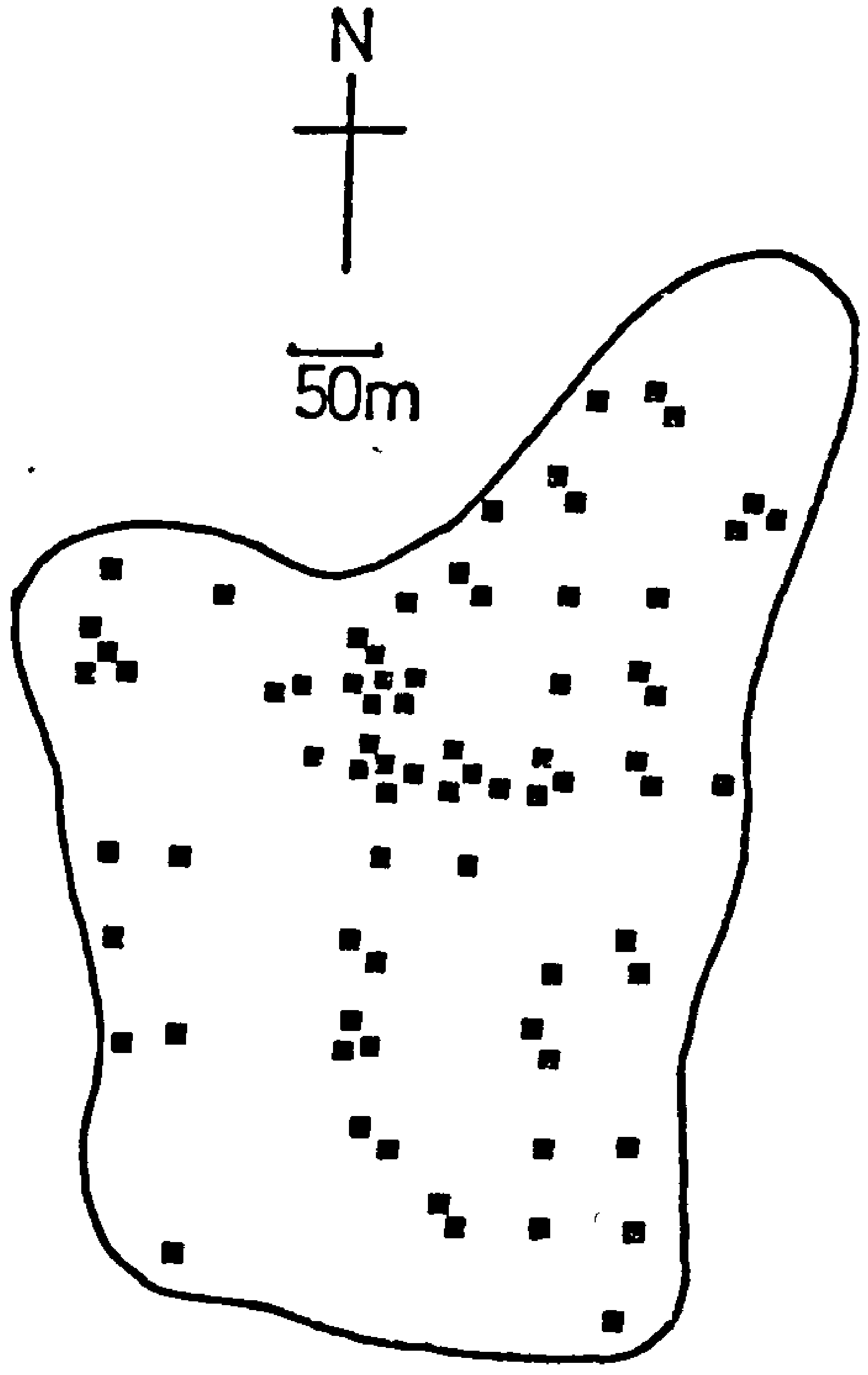
Members of Group V slept close together within each quadrat. Over the whole year 29 (i.e. 41%) of quadrats in the home range were slept in (n=40 nights) and 50% of these were slept in only once. In Group P, over the whole year, 42 (i.e. 60%) of quadrats in the home range were slept in (n=75 nights) and 57% of these were slept in only once.

For Group P sleeping locations in the home range were as dispersed within as between Circuits, and therefore quadrats slept in frequently were chosen at different times of the year. There appeared to be no obvious stochastic relationship between one night's sleeping location and that of the next night, as found, for example by Altmann and Altmann (1970) for *Papio cynocephalus*.

Figure 7.6 Sleeping site location in Group P and Group V. The distribution of sleeping spots is illustrated for each group over the whole year. Each spot represents one night.



Group V



Group P

5. RANGING WITHIN QUADRATS

Movements within quadrats were not closely monitored. The frequency with which individuals changed trees ('tree-changing') was recorded by a Hansen frequency measure - the number of 5-minute periods during which an individual changed trees at least once being noted. This enabled the local movements of individuals and groups to be roughly compared but made absolute frequencies impossible to compute accurately. Individuals did not obviously differ in the mean length of time they were in view at each sighting (see Chapter 2).

5.1. Variation in local movements between groups.

An original suspicion that one group was more active locally than the other was confirmed by measures of tree-changing, adjusted for the amount of time individuals were in view (Figure 7.7). As samples were selected at 30-minute intervals, successive records were likely to be independent of each other and differences were tested (1) between groups ($X^2_{1df} = 23.14$, $p<0.001$) and (2) between each group's combined adults' scores ($X^2_{1df} = 8.51$, $0.001<p<0.01$).[1]

As in many other aspects of behaviour, variation over the year in the frequency of tree-changes was more acute in Group V than in Group P. Differences between the groups were especially marked in the first 4 Circuits. No relationships between the mean number of tree-changes per unit

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[1] Differences between groups were not caused by an overactive infant in Group V as his records were excluded from the analysis.

Figure 7.7 Seasonal changes in the frequency with which individuals in Group P and Group V moved to a new tree. The mean frequency of movements to a different tree executed by each individual daily in each group is represented in A as the observed frequency, and in B when corrected for different visibility of animals in the 2 groups. Both measures are relative and do not represent absolute values of tree-change frequency.


Relative measures of tree-change frequency
A
20
10
0
1 2 3 4 5 6 7 8
Circuit number
Group P
Group V
B
3
2
1
0
1 2 3 4 5 6 7 8
Circuit number
Circuit
I II III IV V VI VII VIII
1972
S O N D J F M A M J J A
1973
Month

time and the proportion of time spent feeding or the frequency with which quadrats were entered were apparent.

5.2. Variation between individuals.

Neither individuals within Group P ($X^2_{1df} = 1.361$ (max), $0.2<p<0.3$), nor within Group V ($X^2_{1df} = 2.26$; $0.1<p<0.2$) differed from one another. Both individuals in Group V, therefore, differed similarly from those in Group P.

5.3. Fine measures of movement.[1]

With the aid of another observer, an attempt was made to record the frequency of a single animal's movements on 4 days, 2 of which were devoted to the adult female of Group P and 2 to the adult male of Group V. On three days complete data were obtained but one period of two hours (when the subject animal was lost from sight) impaired records on the fourth day.

(i) Group P adult female.

During the two days that this individual was observed she could be seen by the observer for 69.9% of the time. As leaping activities were conspicuous the observer probably recorded a greater proportion (than 69.9%) of the leaps executed in this period. From the data presented in Section5.2 this adult female was known to move no more or less than any other individual in her group. During the two days' observations she performed 45 and 50 jump sequences containing from 1 to 9 leaps per sequence and

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[1] I am indebted to Prassede Calabi from Yale University for helping me to collect this data.

totalling 129 and 161 leaps altogether. The total of 290 leaps observed in the 2 days, therefore, occurred in 95 leap sequences - a mean value of 3.1 (made up of 2.9 and 3.2) leaps per sequence.

(ii) Group V adult male.

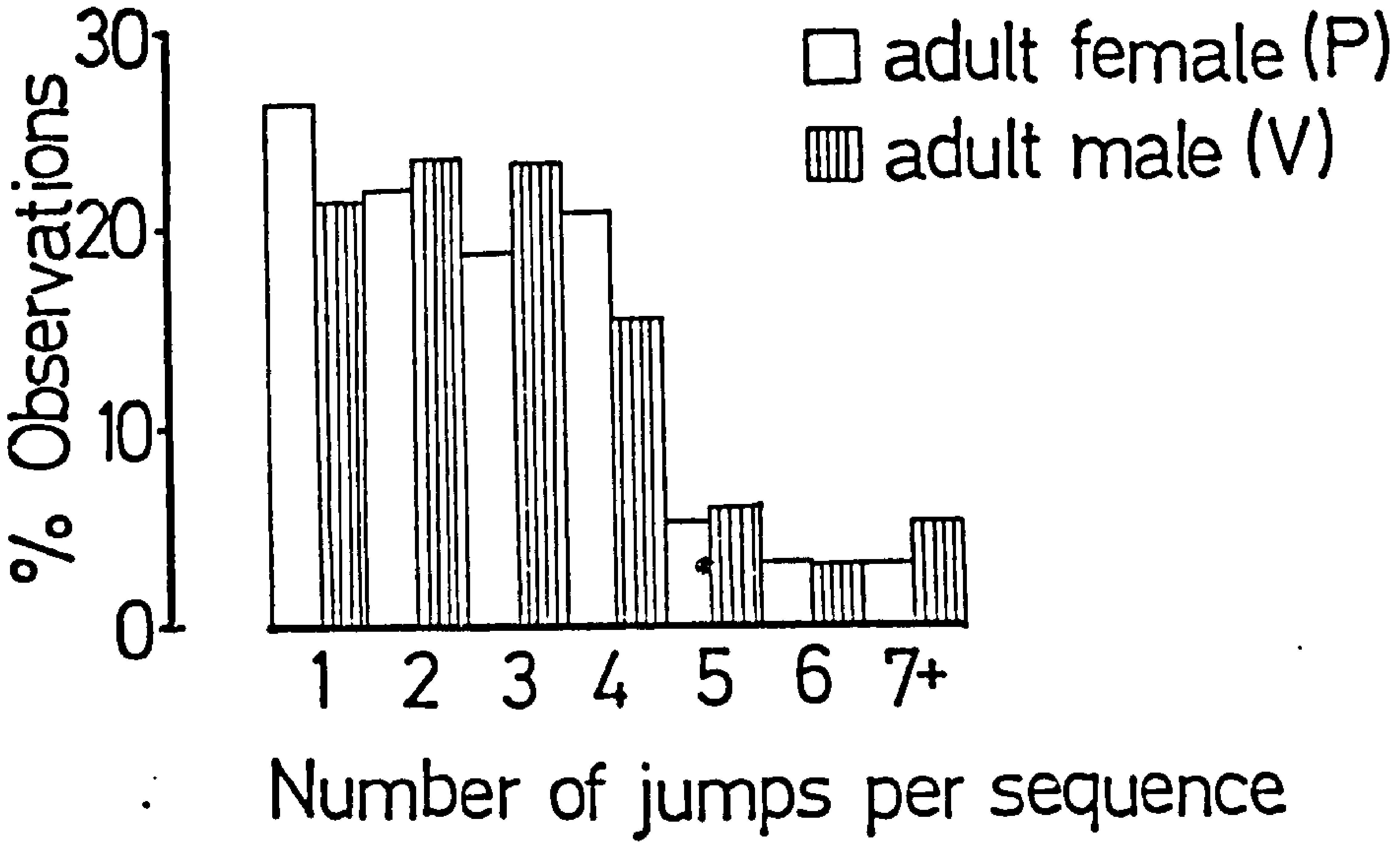
The Group V adult male was seen on the one complete day to make 359 leaps in 112 sequences (mean 3.2 leaps per sequence), and 76 leaps in 23 sequences (3.3 leaps per sequence) on the incomplete day's records. The overall percentage of time this individual was in sight was 80.0%.

It appears therefore that these animals differed not in the type but the frequency of local movements and this conclusion is supported by the distributions of leap sequences for each individual (Fig. 7.8).

Furthermore, 32 leaps were accurately measured for the horizontal distance covered by the adult female of Group P (94.1 ms) and 38 leaps by the adult male (108.1 ms). The mean distances covered by each individual's leaps were similar - 2.9 ms (range 1.3-4.7) and 3.1 ms (range 1.0-6.0) respectively ($t=0.5473$, $0.5<p<0.6$).

Although the data were very limited in quantity there was no reason to think that they were in any way atypical. The threefold difference found in tree-change frequency between the two groups (Fig. 7.7) was echoed by a two to threefold difference in the number of leaps performed. Measurements of the distances covered by leaps were clearly biased against leaps in the middle of

Figure 7.8 The number of jumps in leaping sequences performed by the adult female of Group P and the adult male of Group V.


% Observations
30
20
10
0
1
2
3
4
5
6
7+
Number of jumps per sequence
□ adult female (P)
▥ adult male (V)

leaping sequences or leaps high in the forest, but the direction and probably the extent of these biases were the same for each individual.

Assuming that the leaps were recorded in proportion to the amount of time the animals were in sight overall (see above), the actual distance moved may be calculated. For the Group P adult female this was a mean of 611 ms/day for the two days' data whereas for the adult male it was 1390 ms - over twice as far. The shortest mean distance travelled between quadrats (D) is given by the formula:

$$D = 2. \frac{r/2}{\cos\left(\frac{45^\circ}{2}\right)}$$

where r is the length of one side of a quadrat.

For quadrats of side length 50 metres, D=54.1 ms. During those days when leap sequence frequencies were measured the adult female of Group P moved an estimated 1222 metres. On the same days Group P entered 23 quadrats, travelling a minimum distance of 1190 metres. The very close agreement between the two estimates suggests that the adult female, and indeed the other group members, moved within quadrats only as they moved between them - travelling in straight lines or wide curves about the home range. On the day that data were collected from Group V the group travelled through 9 quadrats (a minimum of 430 ms.), but the adult male actually moved an estimated 1390 metres. As no differences in movement were found between adults, both the adult male and the adult female were moving on average about 3 metres sideways for every 1 metre they moved forward.

6. RANGING BETWEEN QUADRATS

6.1. Introduction.

The organisation of a primate group's movements about its ranging area may be controlled by:

(i) endogenous factors e.g. food attainment motivations, and

(ii) exogenous factors e.g. predator avoidance, defence from conspecifics, seasonal and atmospheric influences.

Both endogenous and exogenous factors have been shown to have varying effects on the ranging behaviour of groups of the same and different species. *Hylobates lar*, for example, regularly sleep in central parts of their territories and move to border regions on average every other day and engage in inter-group encounters (Ellefson 1968,1974). *Cercobeus albigena* move daily at least partly in response to neighbouring groups' movements (Waser 1975). Some lemur species, however, appear to make periodic tours of their home ranges every few days (Jolly 1966). Red colobus monkeys (*Colobus badius tephrosceles*) at Gombe Stream Reserve in Tanzania range primarily so as to diversify their diet (Clutton-Brock 1972,1975) whereas the same animals in the Kibale forest in Uganda are claimed by Struhsaker (1974) to direct their movements mainly according to the location of neighbouring troops.

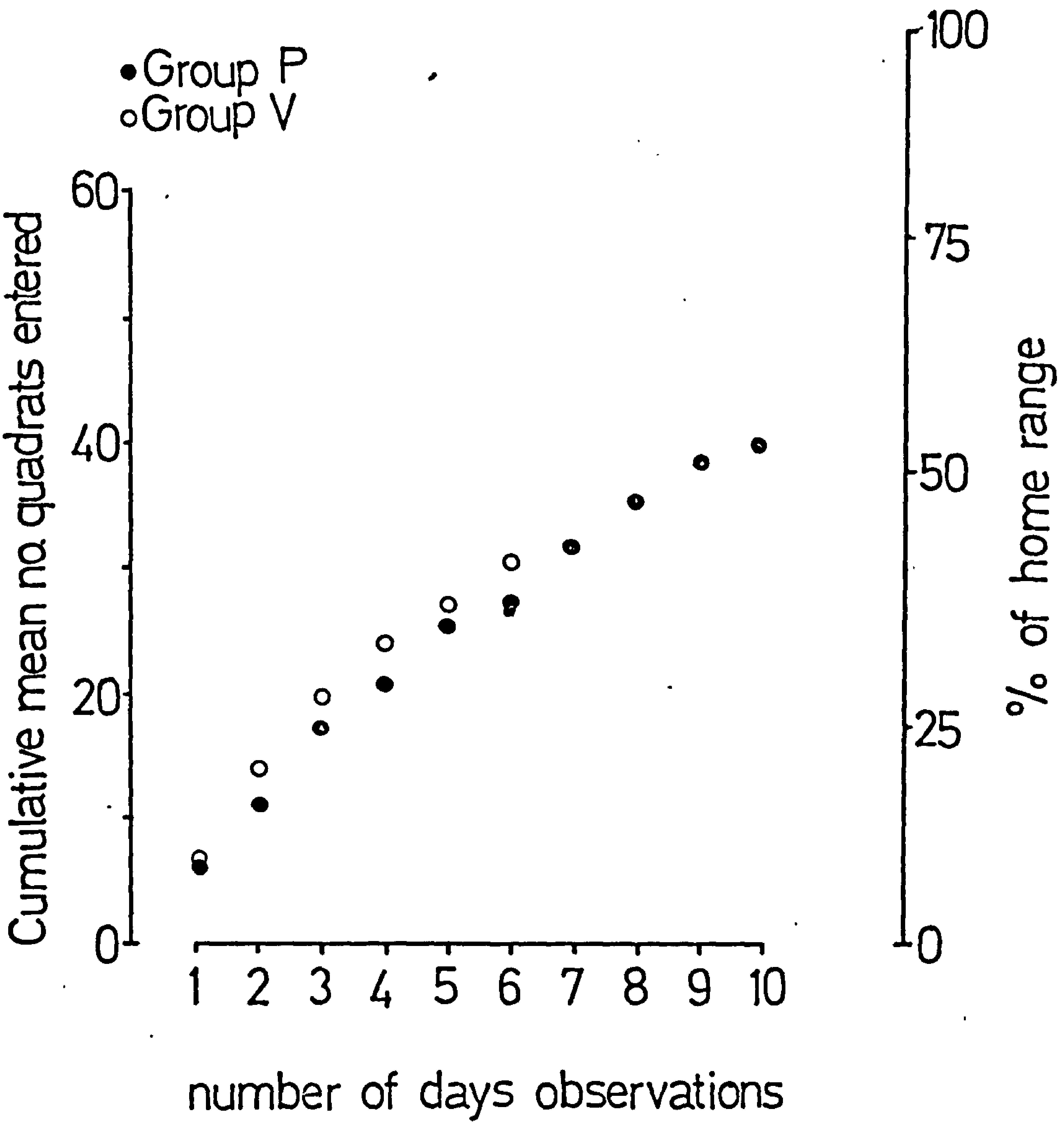
6.2. Indri ranging behaviour.

For *Indri* the observation period each Circuit was too short for long term patterns and seasonal differences of ranging behaviour to be closely examined. In 6 days each group at Analamazoatra moved over mean values of 41.4% (Group P) and 43.5% (Group V) of their home range. These percentages overestimate the proportion of the home range 'covered' by ranging movements as visits to any part of a quadrat is considered, in these calculations, to be visits to the 'whole' quadrat. In 10 days Group P covered a mean of 57.2% of their home range and, by the end of each observation period, were still entering new parts (i.e. parts not having been previously visited during that observation period) at an only slightly declining frequency (Fig. 7.9).

Ranging behaviour was considered to be primarily related to feeding since, with rare exceptions, Indri movements were not associated with overt stimuli or other activities. Members of each of the 2 main study groups usually moved together and a group could, for the most part, be considered as a single feeding unit.

The two distinct forms of 'ranging for food' behaviour observed for this species have been already described (see Chapter 6). Firstly, concentrated food sources in the form of a few neighbouring trees synchronously in fruit or new leaf were visited daily and fed in for several hours - the remainder of the day being devoted to small ranging progressions and shorter feeding bouts on many species. Secondly, the more even ranging and feeding activities of the afternoons (above) could take place throughout the day. These two ranging patterns

<u>Figure 7.9</u> Cumulative mean numbers of different quadrats entered on successive days of the observation period each Circuit, in Group P (10 days) and Group V (6 days).


● Group P
○ Group V
Cumulative mean no. quadrats entered
0
20
40
60
% of home range
0
25
50
75
100
1
2
3
4
5
6
7
8
9
10
number of days observations

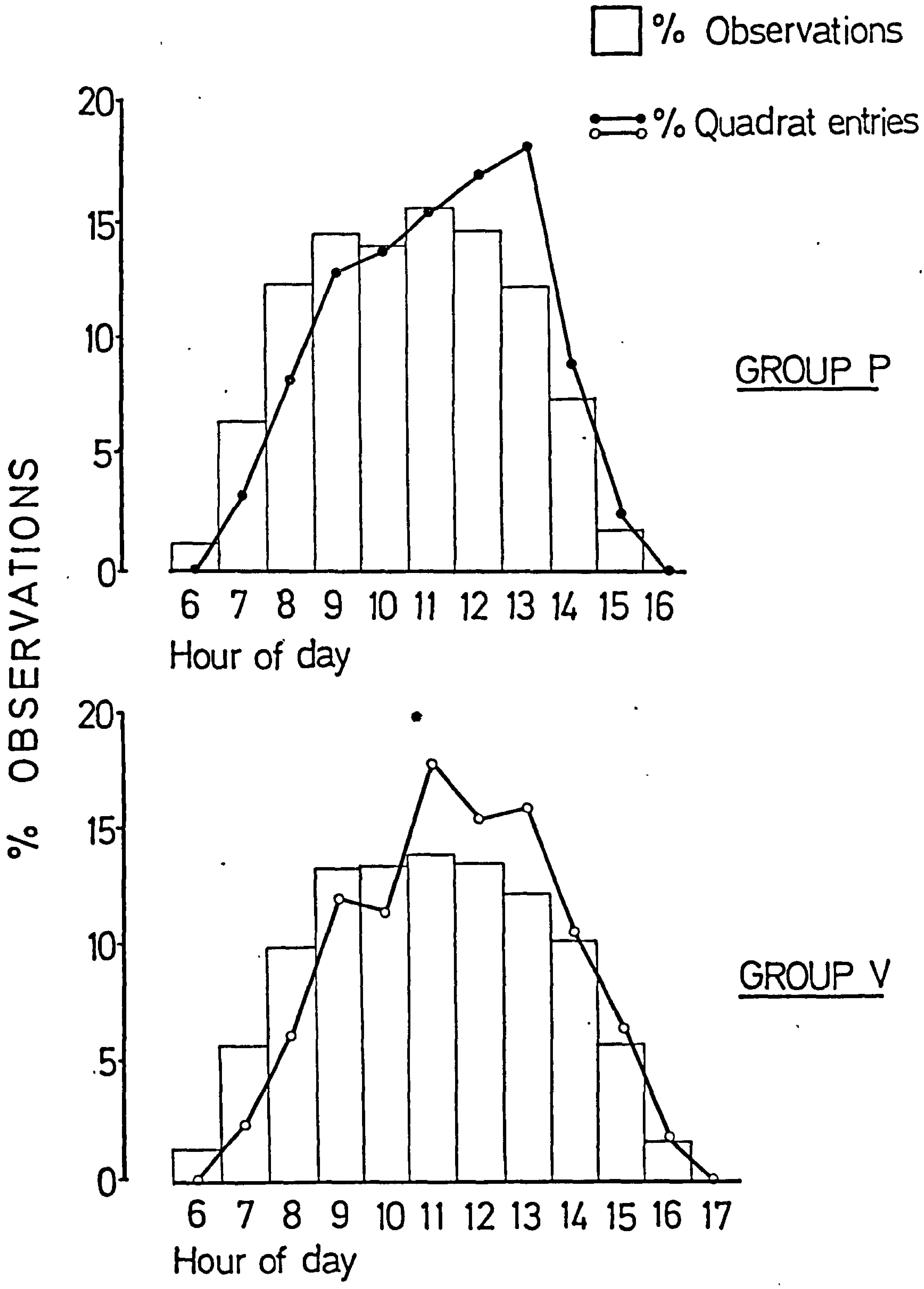
depended on the presence or absence of certain species in the appropriate phenological condition and no gradual seasonal pattern of change from one to the other was apparent (see Chapter 6).

6.3. Temporal distribution of movement.

All members of a group became active at approximately the same time each morning. The first leap by one group member was separated from similar movements or feeding activities in others by only a few minutes. A short feeding bout usually preceded a progression by all group members from their sleeping locations to a defaecation area, where they aggregated. The location of defaecation sites relative to the sleeping area probably defined the direction and distance moved at these times as they were repeatedly used and the group often retraced their steps later in the day, passing by the previous night's sleeping spot.

The temporal distribution of quadrat entry frequencies, from records made at 30-minute intervals, shows a bias towards afternoon progressions (Fig. 7.10). The hours of 1300-1400 contained for Group P the greatest frequency of quadrat entries during Circuits II, III, IV, VI and VII, and the second greatest frequency for Circuits V and VIII. The proportion of quadrat entries made between 1300 and 1400 hours throughout the year were significantly greater than the proportion of observations made in these hours ($X^2_{1df} = 10.755$, $0.001<p<0.01$). Group P moved less than expected about its home range early in the day between 0700 and 0800 ($X^2_{1df} = 4.976$, $0.01<p<0.05$) and 0800 and

Figure 7.10 Hourly distribution of entries to quadrats and the hourly distribution of observations in Group P and Group V throughout the year.


% Observations
% Quadrat entries
% OBSERVATIONS
20
15
10
5
0
6 7 8 9 10 11 12 13 14 15 16
Hour of day
GROUP P
20
15
10
5
0
6 7 8 9 10 11 12 13 14 15 16 17
Hour of day
GROUP V

0900 ($X^2_{1df} = 5.06$; $0.01<p<0.05$).

Although no hour-by-hour differences in ranging activity (compared to the proportion of observations) could be determined for Group V (probably due to sample size shortcomings), there existed a similar tendency to move more in the afternoon than in the morning. If morning (<1200 hours) and afternoon (>1200 hours) quadrat entry frequencies are compared in the two groups, the latter are found to be superior both for Group P ($X^2_{1df} = 13.224$, $p<0.001$) and for Group V ($X^2_{1df} = 4.00$; $0.01<p<0.05$).

6.4. Distances moved by Indri at Analamazoatra.

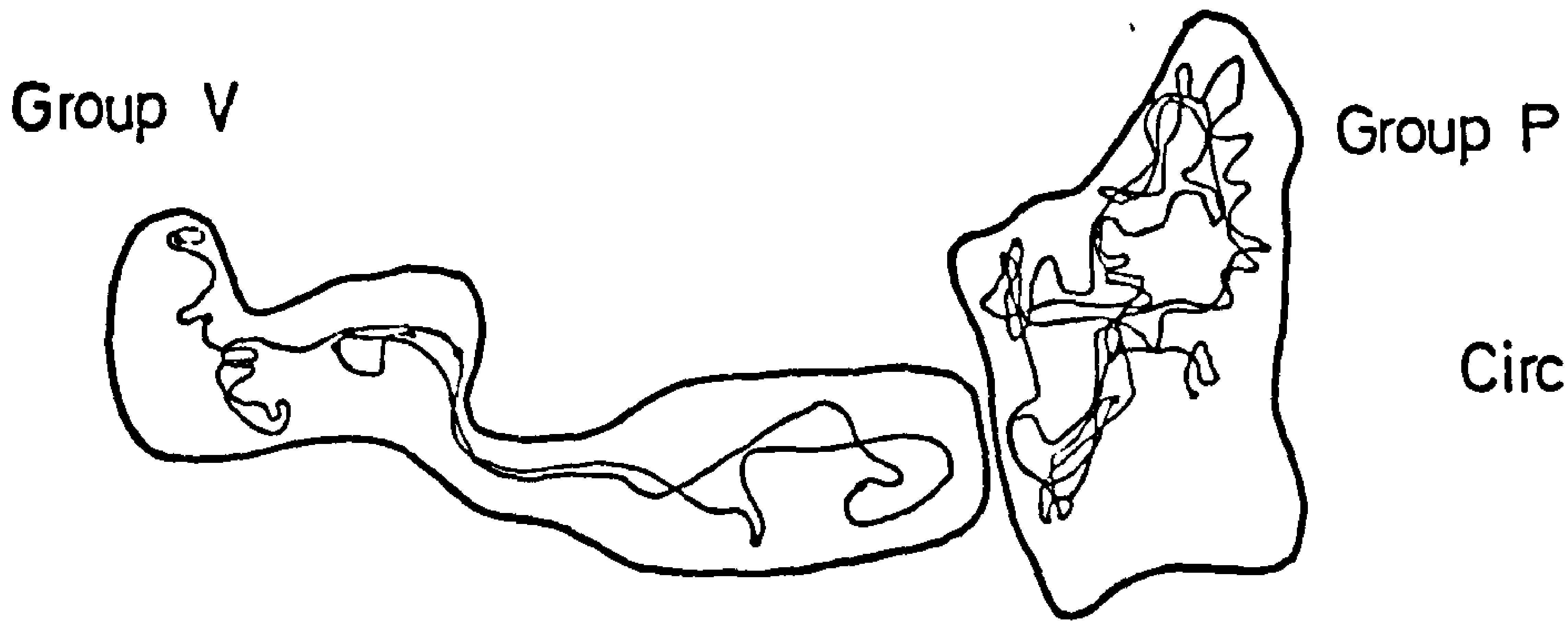
The complete ranging pattern of each study group during each Circuit except Circuit I[1] is shown in Figure 7.11. Much of Group P's home range, if one considers large divisions of the home range, was visited each Circuit. The specific use of certain parts during Circuit IV represents the main departure from this general rule, and it was at this time that Group P repeatedly visited, day after day, large fruit trees in the north-west and south-west of the home range.

It is impossible to state whether the distinct ranging patterns of Group V in Circuits VII and VIII were typical of those months, whether these were "anomalies" resulting from the short observation period (6 days), or

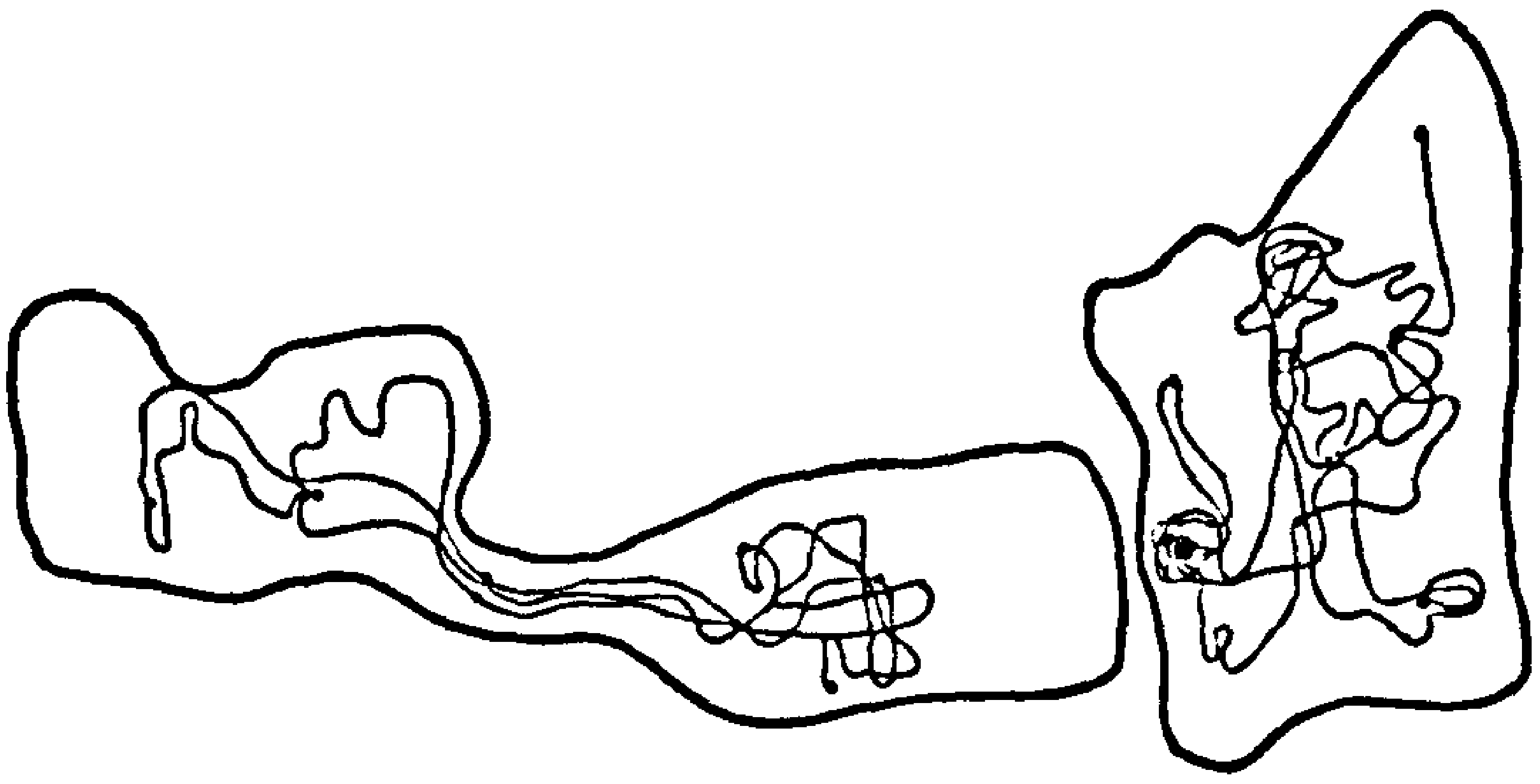
---

[1] Group V moved outside the original set of marked quadrats in Circuit I and these were subsequently extended before Circuit II observations were begun. Group V never moved outside the 'extended' grid system in following Circuits.

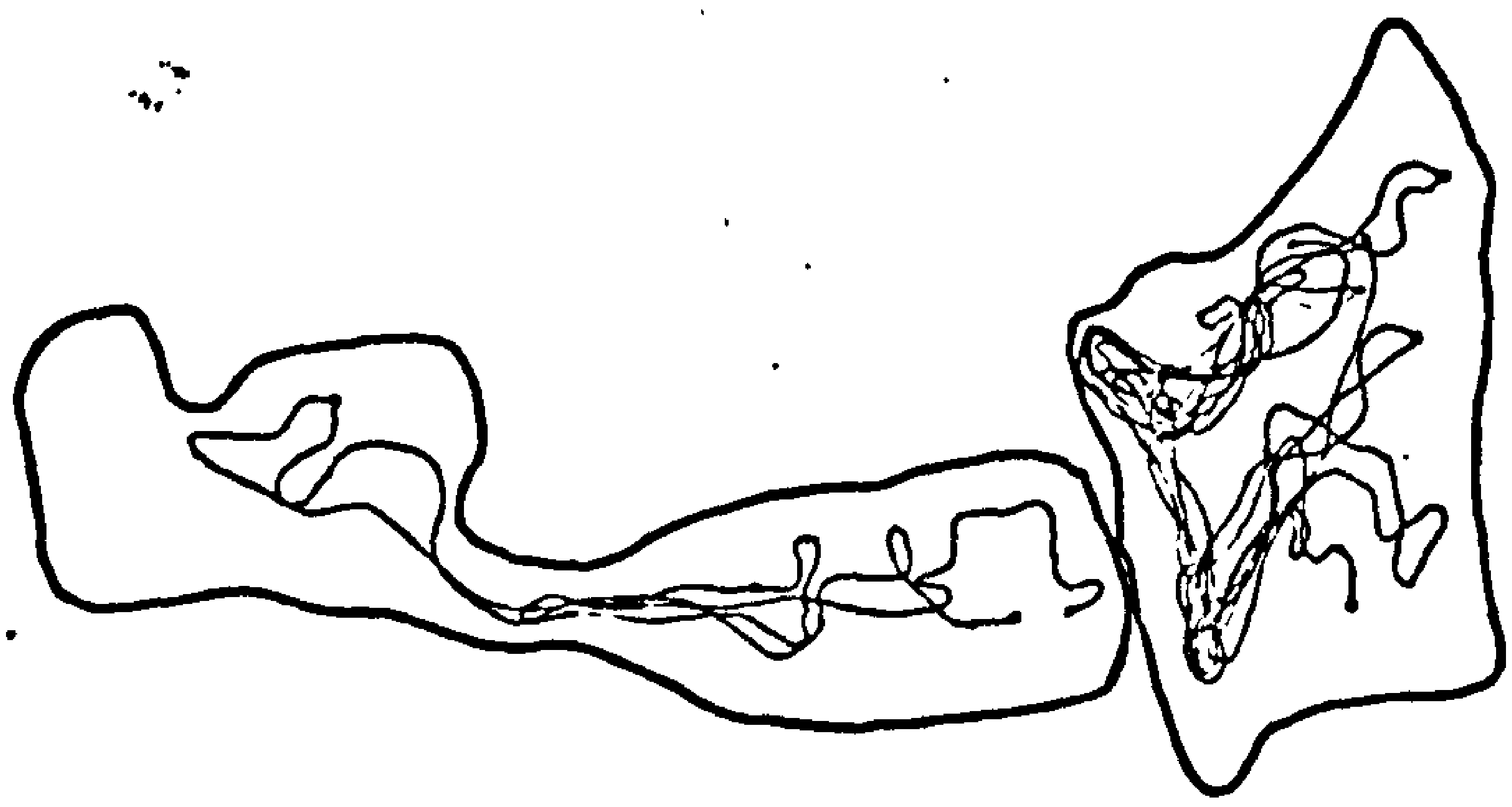
Figure 7.11 Ranging patterns for complete Circuits for Group P (10 days) and Group V (6 days) at Analamazoatra. Each spot represents a night sleeping site.



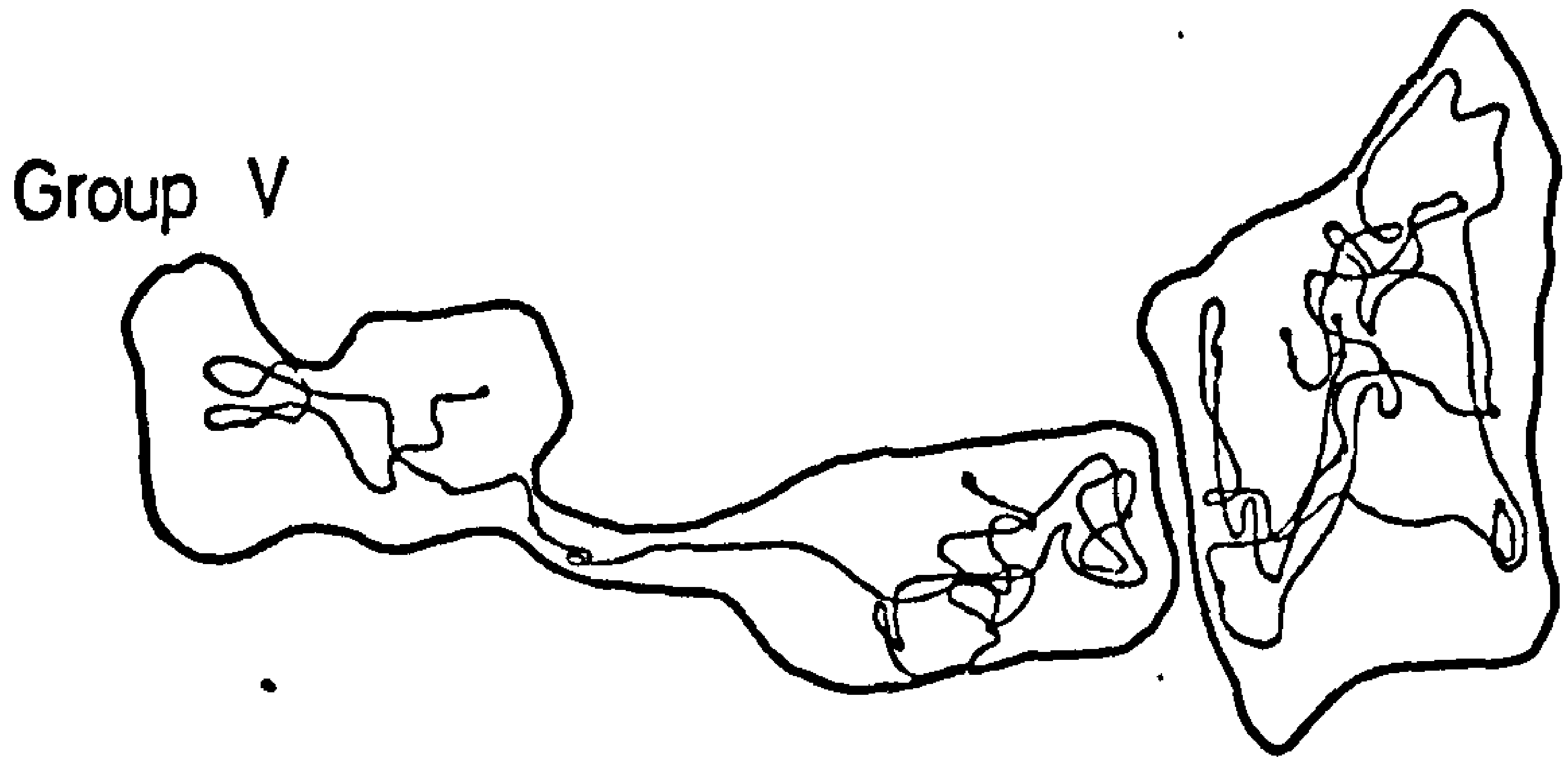
Circuit II



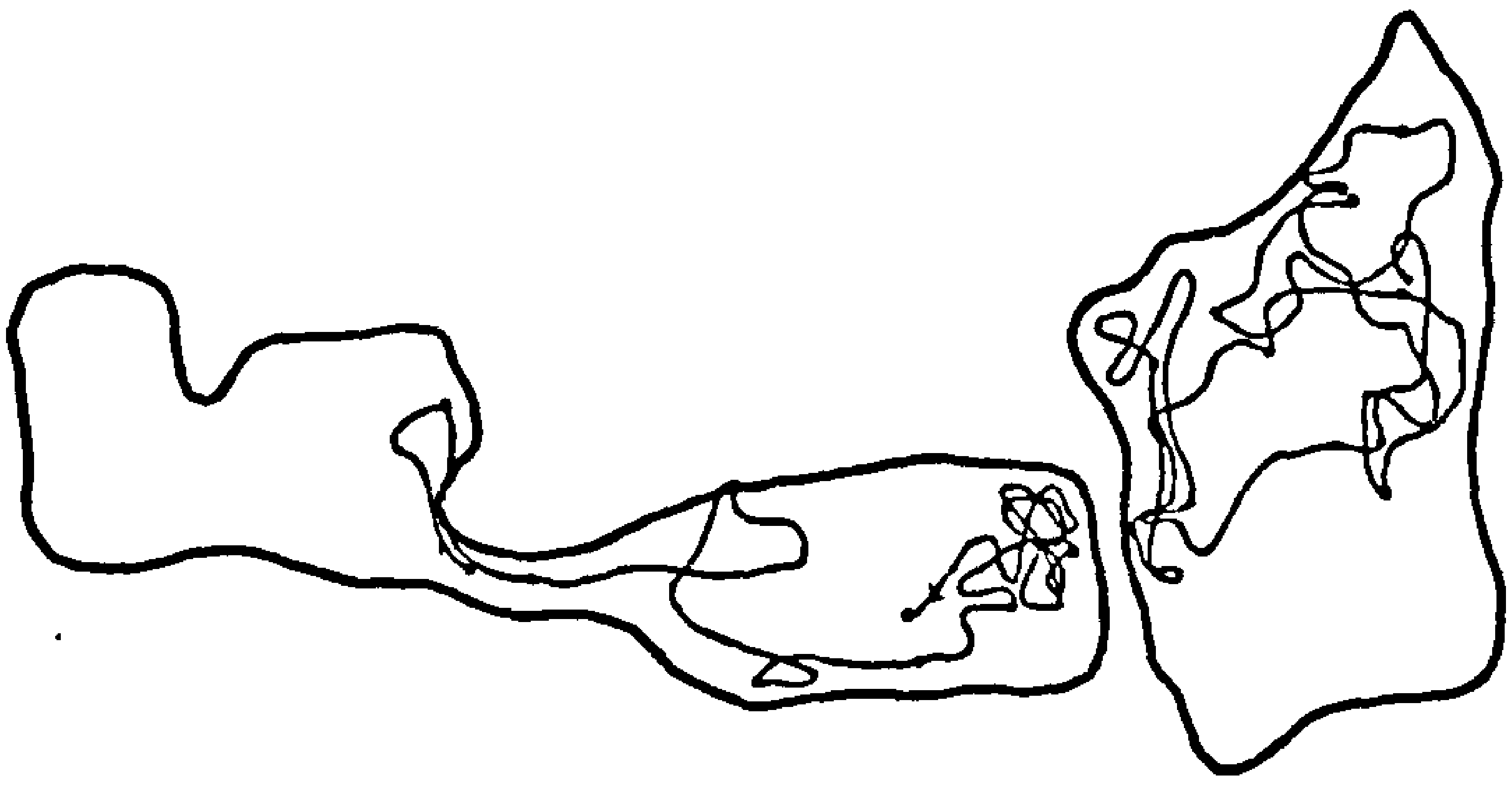
Circuit III



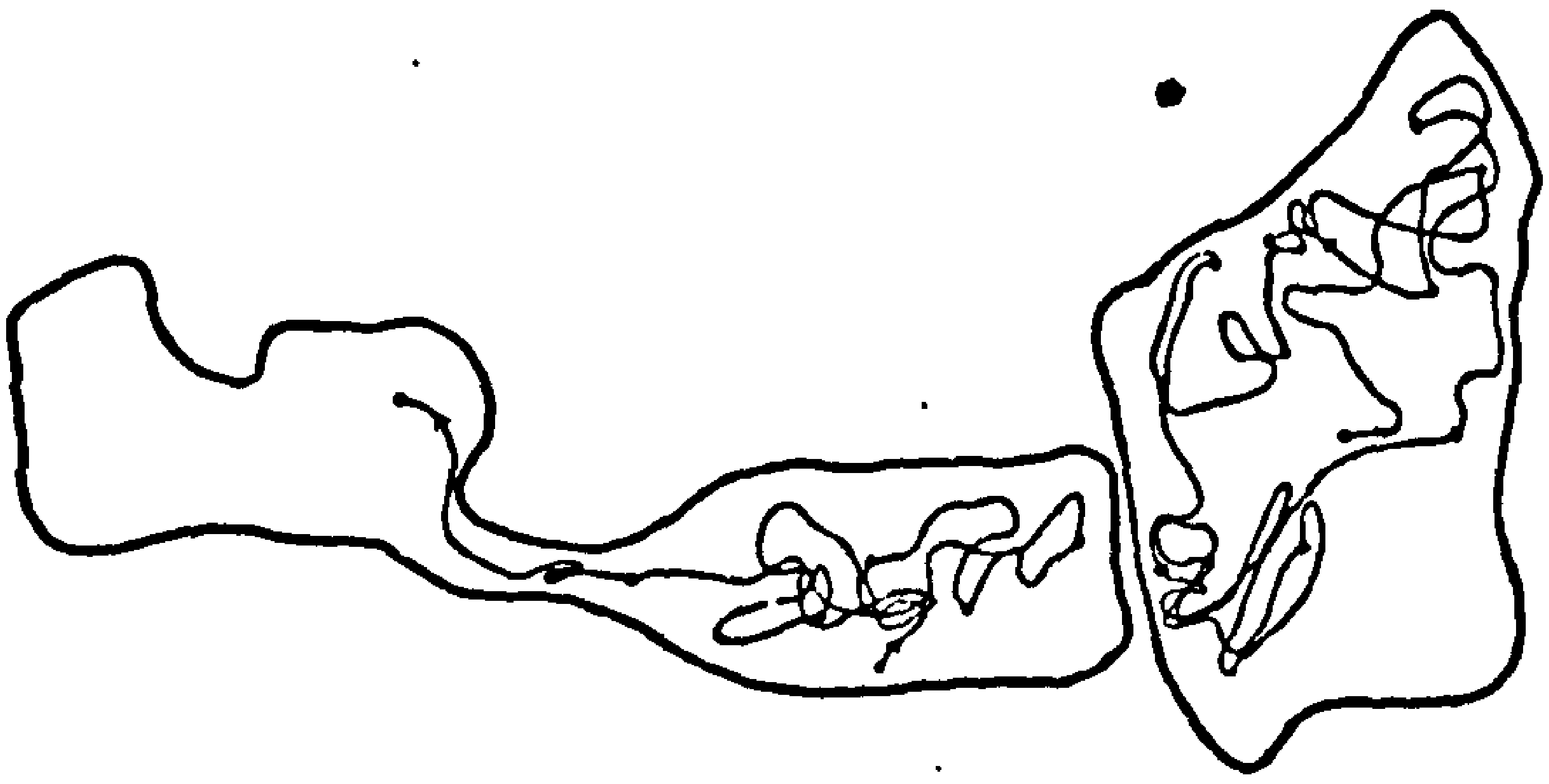
Circuit IV



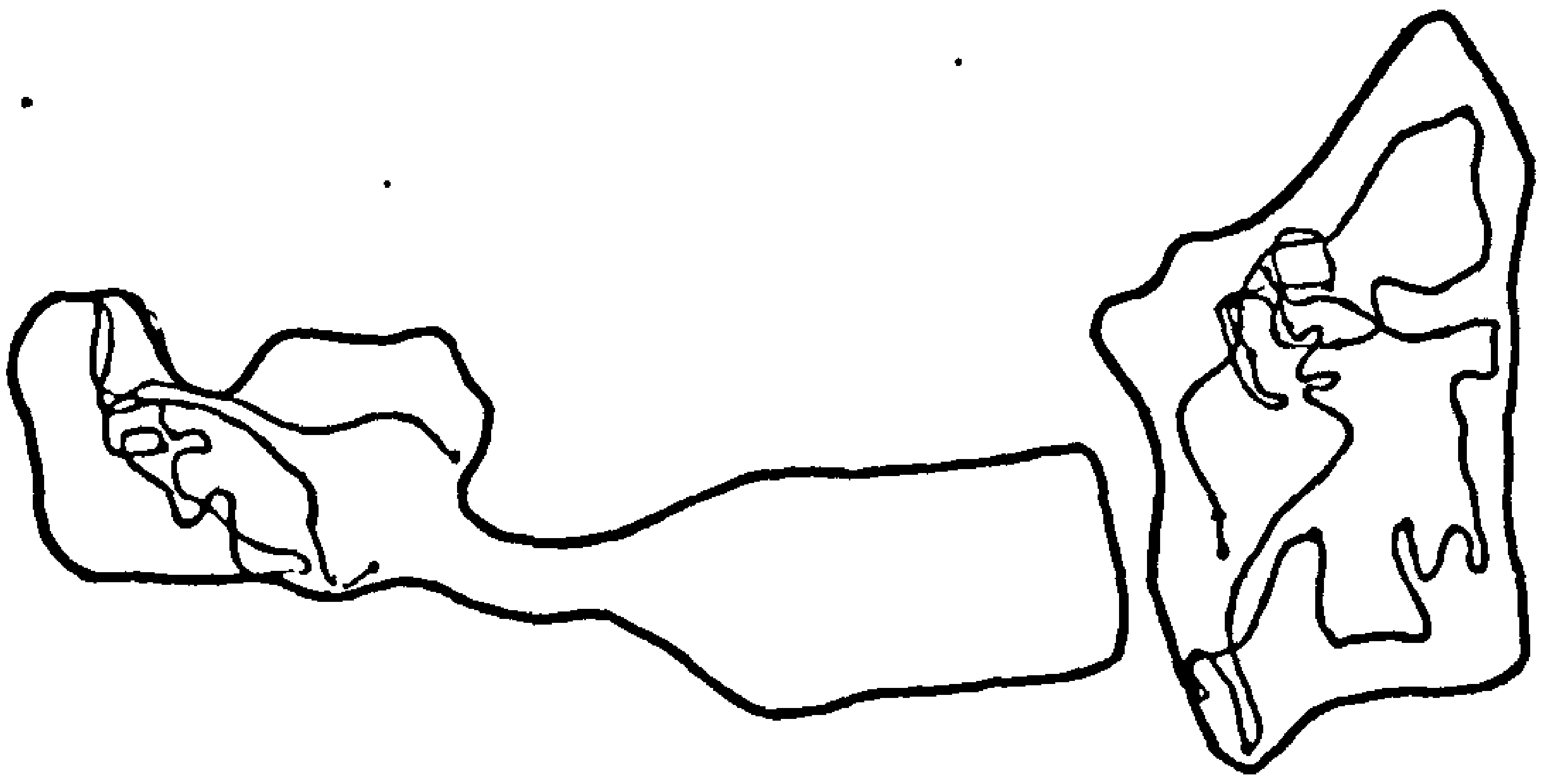
Circuit V



Circuit VI



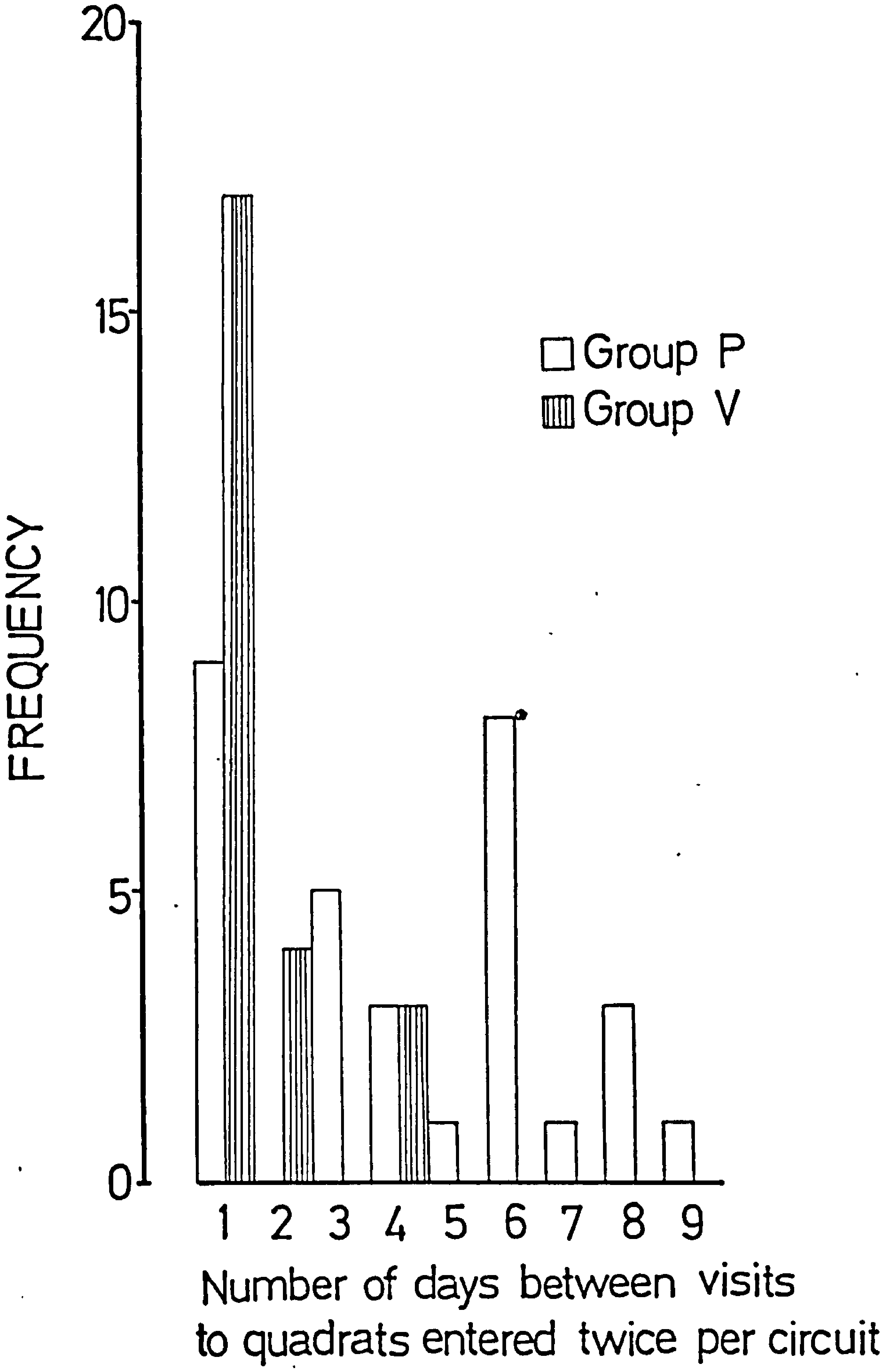
Circuit VII



Circuit VIII

whether they derived from a sampling 'error'. If a group of animals is difficult to find and does not travel across a large part of the home range during the observation period, measures of ranging will be influenced by the position of their first sighting. There was no obvious indication, however, that Group V could be found in some parts of their home range more easily than in others, although for Group P this was probably true. Records of ranging were not biased for Group P as a result of this factor because this group could always be found within one day and quantitative records were only commenced each Circuit the day after the animals had been found. Furthermore, apart from Circuit IV those parts of the home range visited on one day (represented by those quadrats entered) were not dependent on those visited the previous day. To prove this, on all those occasions when quadrats were entered only twice in a Circuit, and where these were not quadrats which (for geometrical reasons) had to be revisited in order for ranging to continue, the interval between visits was computed. The distribution of interval-days (Fig. 7.12) was plotted and the numbers of instances where these were scored as more or less than the expected mean value, were compared for each group. A Binomial test executed on the data showed that interval-days did not vary more than expected by chance for either Group P ($0.1<p<0.2$) or Group V ($0.3<p<0.5$). For most of the year, therefore, Group P were not ranging in consistent patterns of movements repeated daily.

Figure 7.12 Distributions of the numbers of days between visits to quadrats entered only twice each Circuit over the whole year for Group P (10 days) and Group V (6 days).


20
15
10
5
0
FREQUENCY
☐ Group P
▥ Group V
1 2 3 4 5 6 7 8 9
Number of days between visits to quadrats entered twice per circuit

The mean number of quadrats entered each day for the whole year was 8.7 for Group P and 9.5 for Group V. The total numbers of quadrats, the numbers of new quadrats (quadrats which had not been previously entered that day), and the median number of quadrats entered daily all showed highly variable distributions between Circuits that were composed either of a progressive decrease throughout the study period or a basic seasonal difference (Fig. 7.13). The numbers of quadrats entered during the summer Circuits were probably higher than those entered during the winter Circuits for both groups, reflecting the greater activity during these months.

The daily distribution of new quadrat entries for the two groups (Fig. 7.14) ranged from 3 to 13 for Group P and 3 to 17 for Group V. Inter-group variation in central tendency of this measure was examined by a Median test and found to be not significant ($0.1<p<0.2$).

Attempts to compare ranging distance between the two groups confront two major difficulties:

(i) By coincidence heavy rain (which reduced all activities) differed greatly between the two groups' observation periods, falling much more often whilst I was watching Group P than Group V.

(ii) The activity period of Group V was longer than that of Group P (see Chapter 3).

These factors may or may not have caused the small difference in the numbers of quadrats entered by the two groups at Analamazoatra. Approximate measures of real

Figure 7.13 Seasonal variation in the mean and median numbers of (1) all, and (2) different quadrats entered daily for Group P and Group V.

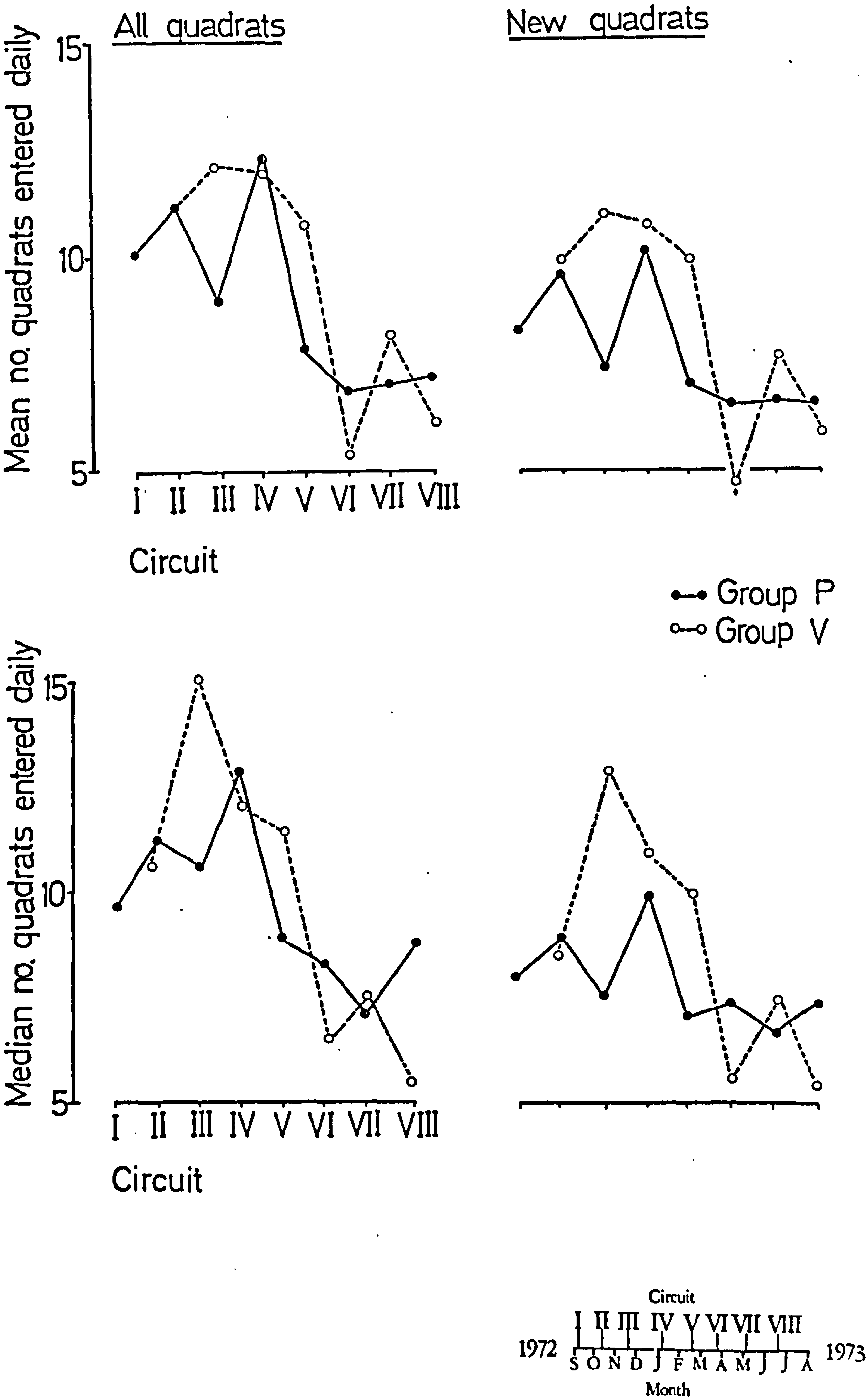
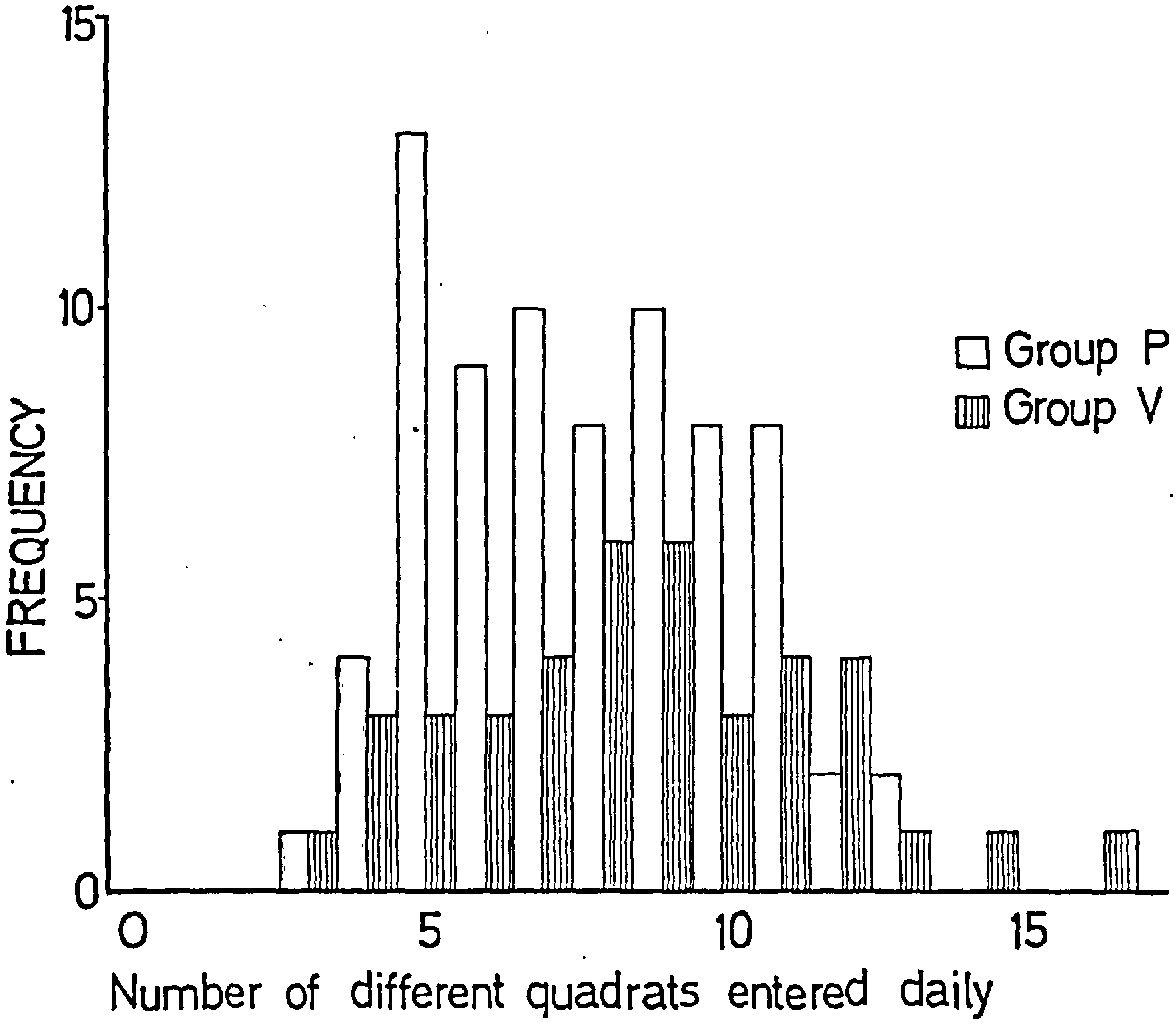

All quadrats
New quadrats
Mean no. quadrats entered daily
15
10
5
I
II
III
IV
V
VI
VII
VIII
Circuit
Group P
Group V
Median no. quadrats entered daily
15
10
5
I
II
III
IV
V
VI
VII
VIII
Circuit
Circuit
I II III IV V VI VII VIII
1972
S O N D J F M A M J J A
1973
Month

Figure 7.14 The numbers of different quadrats entered daily over the whole year for Group P and Group V.


15
10
5
0
FREQUENCY
□ Group P
▥ Group V
0
5
10
15
Number of different quadrats entered daily

distance moved may be calculated from the formula for the shortest mean distance between the centres of two quadrats (54.1 ms), and these are presented in Table 7.2 .

Variation in the total numbers of quadrats entered between Circuits was examined in both groups by a Kruskal Wallis One Way Analysis of Variance which suggested significant differences in Group V ($H=19.26$, $df=6$; $0.001<p<0.01$) but not for Group P ($H=10.1$, $df=6$; $0.1<p<0.2$). When only those quadrats which had not been previously entered each day are examined, neither group exhibited a significant variation (Group P: $H=4.6$, $df=6$; $0.5<p<0.7$. Group V: $H=8.4$, $df=6$; $0.2<p<0.3$). This result, suggests that Group V were revisiting quadrats within Circuits more than Group P.

The overall tendency to revisit quadrats appeared, however, not to differ between the two groups (Fig. 7.15). The numbers of quadrats visited more than once each Circuit ranged from 7 to 18 (21%-49% of the total numbers of quadrats entered that Circuit) for Group P, and 8 to 22 (35% to 55% of the total number of quadrats entered that Circuit) for Group V. The number of quadrats entered only once during a Circuit was also very similar in the two groups (Fig. 7.16). It was, therefore, the slightly greater seasonal inconsistency in quadrat re-entry frequency that constituted the main discernable difference between the two groups' ranging patterns.

It has been shown in previous Chapters that other aspects of the behaviour of Group V varied more between

Circuit	(Gp)	I	II	III	IV	V	VI	VII	VIII
Mean number of quadrats entered	P	10.0	11.2	9.0	12.4	7.9	6.9	7.1	7.3
	V	-	11.2	12.2	12.0	10.8	5.3	8.2	6.2
Estimate of distance in metres	P	541	606	487	670	428	374	385	395
	V	-	606	660	650	585	286	443	336

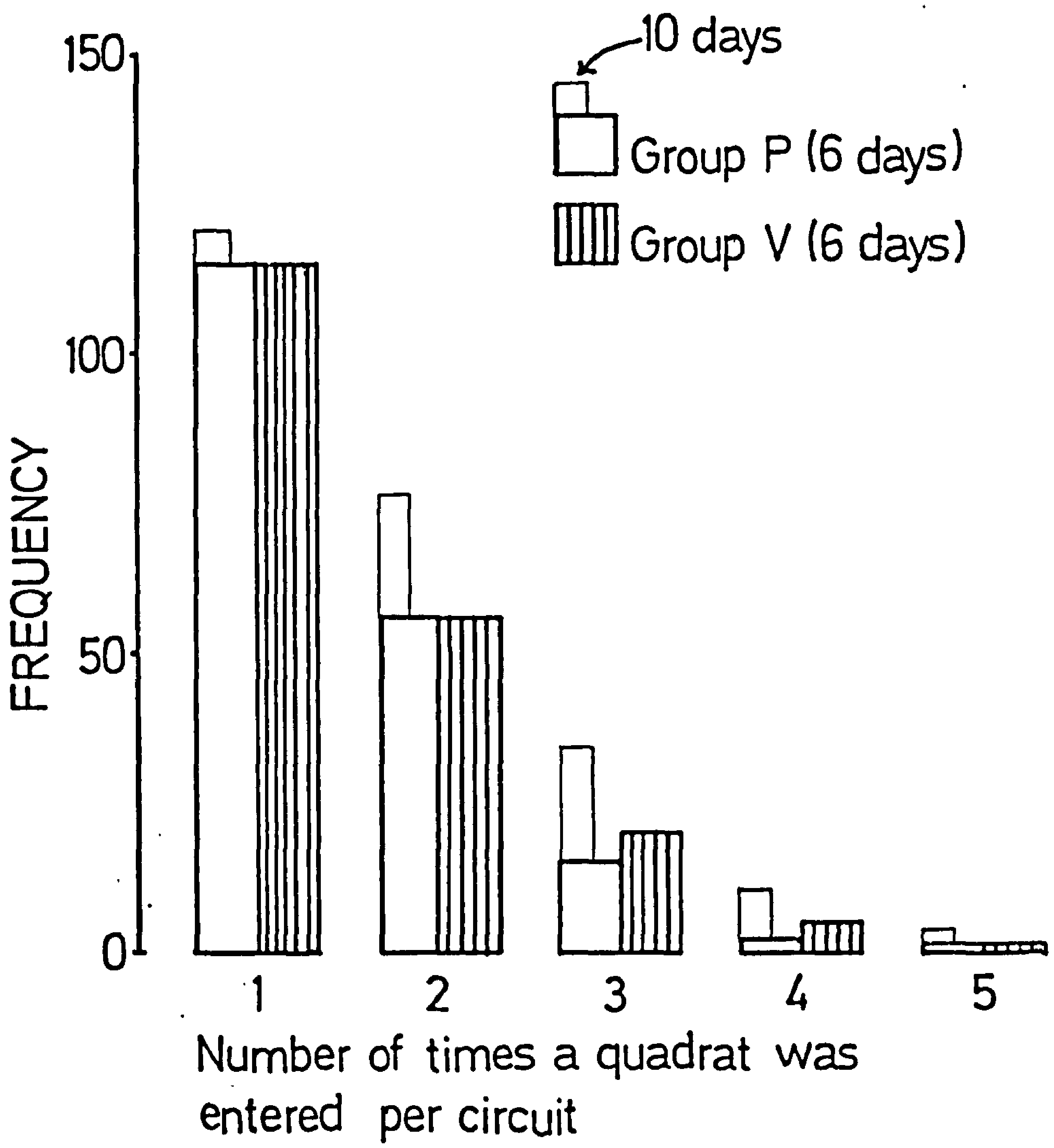
TABLE 7.2. Mean distance travelled daily by the 2 study groups at Analamazoatra for each Circuit.

	GROUP P		GROUP V	
	Ad ♀	Ad♂	Ad♀	Ad♂
r^s	0.04	-0.25	-0.64	-0.82
p	NS	NS	NS	<0.05 >0.01

n=7

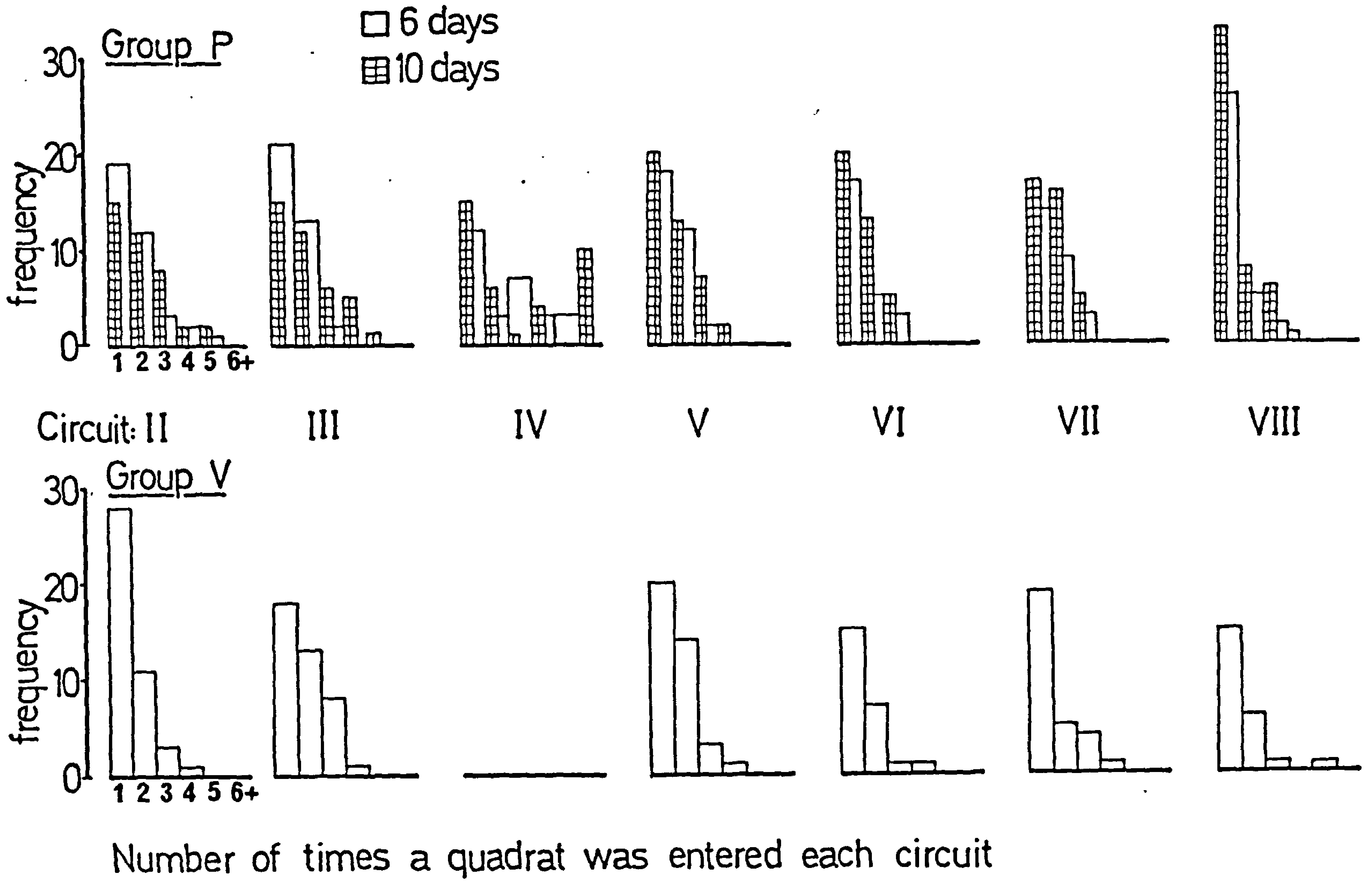
TABLE 7.3. Spearman Rank correlation coefficients between the proportion of angled ranging movements and adults' feeding time.

Figure 7.15 The number of times a quadrat was entered each Circuit over the whole year for Group P (10 days and 6 days) and for Group V.



10 days
Group P (6 days)
Group V (6 days)
150
100
50
0
FREQUENCY
1
2
3
4
5
Number of times a quadrat was entered per circuit

Figure 7.16 Seasonal variation in the number of times a quadrat was entered for Group P (10 days and 6 days) and for Group V.


Group P
□ 6 days
▦ 10 days
frequency
30
20
10
0
1 2 3 4 5 6+
Circuit: II
III
IV
V
VI
VII
VIII
Group V
frequency
30
20
10
0
1 2 3 4 5 6+
Number of times a quadrat was entered each circuit

Circuits than Group P. The proportion of the activity period spent feeding by this group (Group V), was not, however, significantly correlated with the number of quadrats entered ($r^s = 0.57$, n = 6), the number of quadrats revisited ($r^s = 0.03$, n = 6) or the number of quadrats entered only once ($r^s = 0.31$, n = 6).

Differences between 6 and 10 day samples for Group P show the changing relationship between quadrat entry and re-entry over the observation period each Circuit. The tendency to revisit a quadrat between days 6 to 10 of the observation period each Circuit that had been first entered between days 1 and 6, is illustrated in Fig. 7.15. It is seen that this tendency is greater for quadrats that had been previously visited several times than for those that had been visited only once. Thus although the tendency to visit new parts was declining as the observation period progressed, revisited parts were more likely to be re-entered many times than simply once.

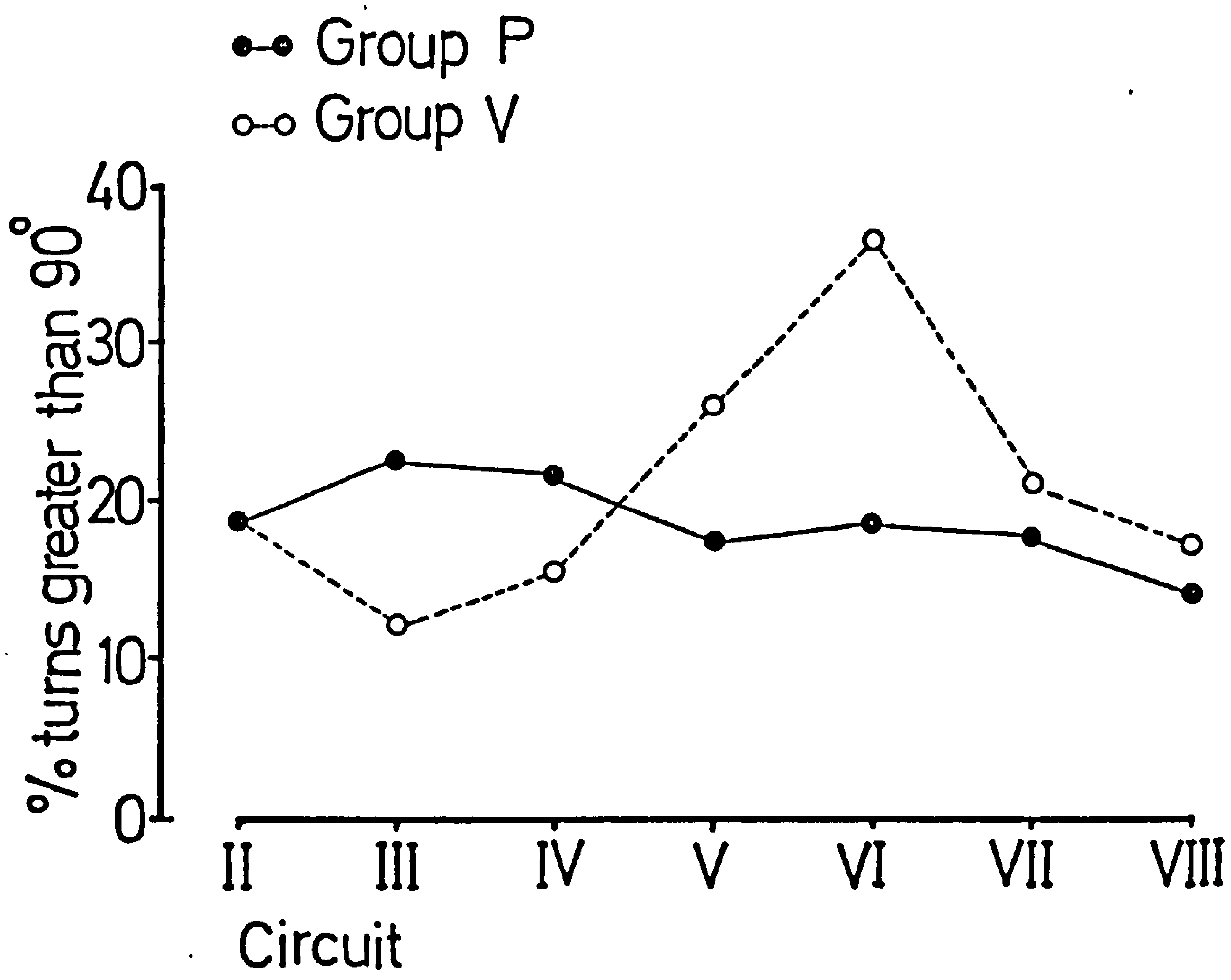
6.5. Ranging Continuity.

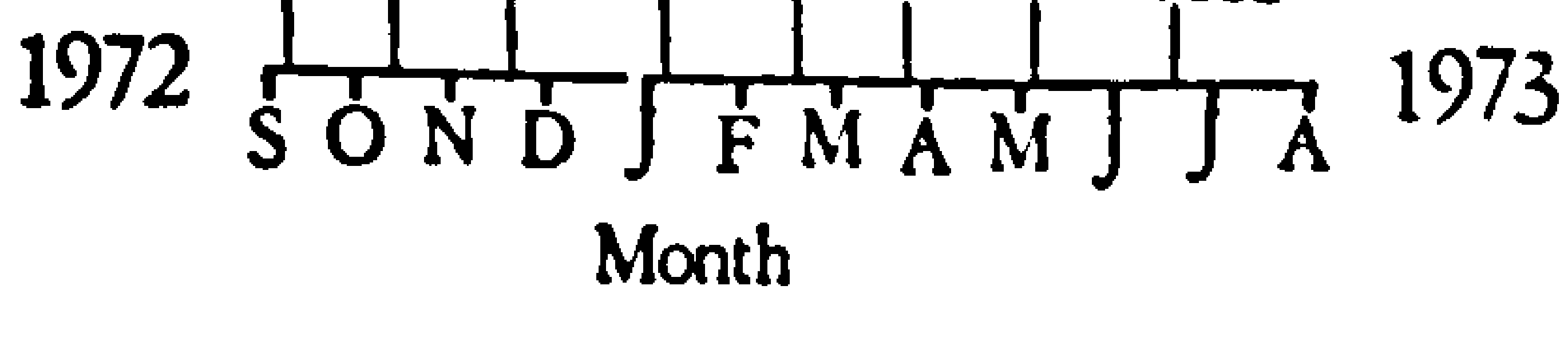
Previous sections have presented evidence suggesting that although Group V moved 2-3 times as frequently within quadrats as Group P, movement between quadrats was essentially similar. Group V, it was suggested, moved about 3 metres 'sideways' for every metre they moved 'forwards'. In order to find out whether this local tackling movement in Group V was carried through into their ranging patterns, the tendency to move in approximately straight lines ("ranging continuity") was examined in both groups. The proportions of quadrat changes involving angled turns away from the direction taken by the group in order to enter that quadrat, were computed for turns of less than or greater than 90° (Fig. 7.17). Turns of greater than 90° occurred in 20.0% and 19.0% of the movements between quadrats for groups V and P respectively. No differences between groups in this measure could be found for any Circuit (X^2_{1df}= 2.0536(max); $0.1<p<0.2$). Differences in the shape of the study groups' home ranges may have reduced the ability for Group V to turn acutely, and real differences may, therefore, have existed.

Seasonal variation in the proportion of angled turns made was greater in Group V than in Group P. Attempts were made to correlate the frequency of angled turns with the proportion of time each group spent feeding each Circuit. These were found to be non-significant for Group P (r^S=0.07, n=7) but significant at the 5% level for Group V (r^S=0.75, n=7). To see whether this relationship could hold for individuals as well as groups, tests were made to relate the proportion of time spent feeding by each adult with its group's frequency of angled turns (Table 7.3). It is concluded that the more frequently that angled turns were made, the smaller the proportion of time the adult male of Group V spent feeding.

Seasonal changes in the frequency of angled turns made by Group V is also negatively correlated with the mean number of quadrats entered (r^S=0.752, n=7; $0.01<p<0.05$).

Figure 7.17 Seasonal variation in the proportion of acutely angled turns made by Group P and Group V when moving from one quadrat to another.


●-● Group P
○-○ Group V
% turns greater than 90°
40
30
20
10
0
II
III
IV
V
VI
VII
VIII
Circuit


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S O N D J F M A M J J A
1973
Month

The more turns this group made, therefore, the fewer quadrats were entered. Quadrats were visited more than once approximately equally over the year (see Fig. 7.15) and the peak in angled turns at Circuit VI was not correlated with exceptional numbers of quadrat revisitations. This group was apparently, therefore, making a greater number of acutely angled turns when it moved the least, rather than turning to revisit specific areas.

6.6. External influences on ranging behaviour.

6.6.1. Weather.

Observations were of too short a duration and ranging variability too great to examine the effects of weather on quadrat entry frequencies. During continuous heavy rain all activities ceased and the animals would remain in sleeping positions for most of the day. Light rain or short dispersed periods of heavy rain, however, did not obviously influence ranging activities.

For 4 of the 8 Circuits Group P entered most quadrats on days when least rain fell. During 5 of the 8 Circuits fewest quadrats were entered on days when most rain fell. The polarity of the relationship is thus well defined. Within Circuits, however, on only 1 day was the median number of quadrats entered associated with the median proportion of time that rain fell.

As Group V were observed on only 2 very wet days no similar relationship between weather and movement can be demonstrated. It is clear, however, that the greater variability found in Group V's quadrat entry frequency over the year was not due to changing weather conditions.

6.6.2. Social aspects.

The use of loud calls to effect spacing has been demonstrated for Alouatta palliata (Chivers 1969), Cercocebus albigena (Waser 1975) and has been proposed for many other species (Marler 1968). The relationship between territory definition and Indri song is discussed in Chapter 9, but it was considered possible that ranging patterns were dependent in some way on the positions of neighbouring groups. Informative parameters of other groups' positions were probably transmitted by their vocalisations, which often induced calling in the study groups.

To investigate the possible influence of other groups on the ranging pattern of the group under study, the direction in which the study group moved following calls within 1000 metres was recorded for those times of the year when vocal activity in the population was both high (summer) and low (winter). The results (Table 7.4) indicate that no overt influence by the calls of neighbouring or nearby Indri groups on the study group's movements could be demonstrated.

Although a group was always seen to divide during a confrontation with another group, the adult males (of the 2 groups) approaching each other at the territorial border (see Chapter 9), this was always followed by a rapid

Movement:	NEARER to calling source	FURTHER from calling source	TOTAL
HIGH	17	19	36
LOW	8	9	17
TOTAL	25	28	53
%	47	53	100%

$X^2_{1df\,(overall)} = 0.0001;\ 0.98 < p < 0.99$

TABLE 7.4. Direction of movement by Group P in response to calls within 1000 metres in two seasons.

return to the normal cohesive group formation and subsequent ranging activities were not seen to be affected in any way.

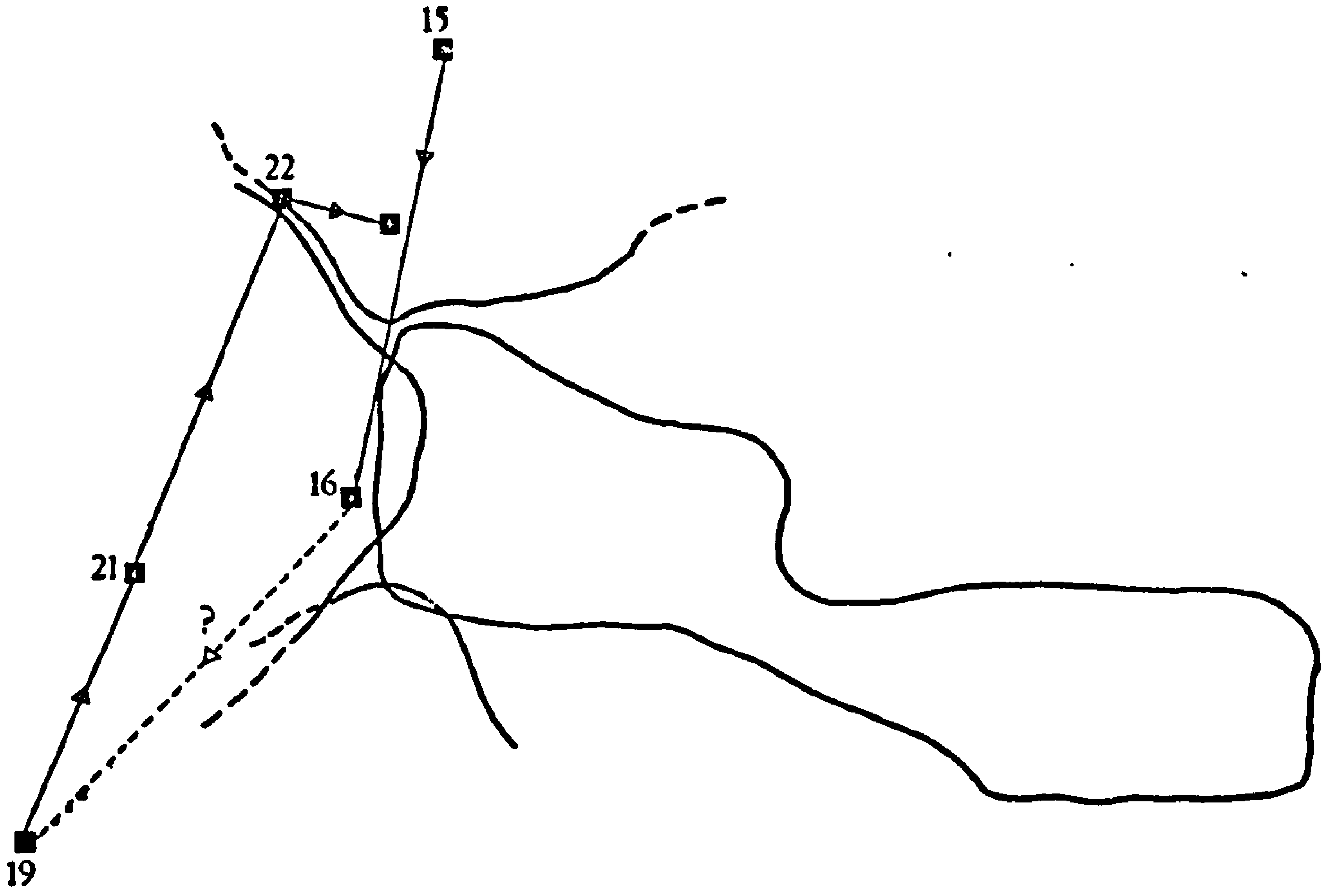
6.6.3. Predators.

Large terrestrial carnivores such as *Cryptoprocta ferox* were dispersed by the observer when following the two study groups at Analamazoatra. Observations on Group IV at Vohidrazana could be made, however, from a position where my presence could be detected neither by *Indri* nor by other species, and no interactions with any predator was witnessed. Birds, thunder, aeroplanes and people could cause *Indri* to cease activity, but subsequent movements were not obviously affected in any way. *Indri*'s reaction to humans and dogs first perceived at short distances was to flee for about 100 metres. If pursued the animals would continue to flee to the other side of their home range.

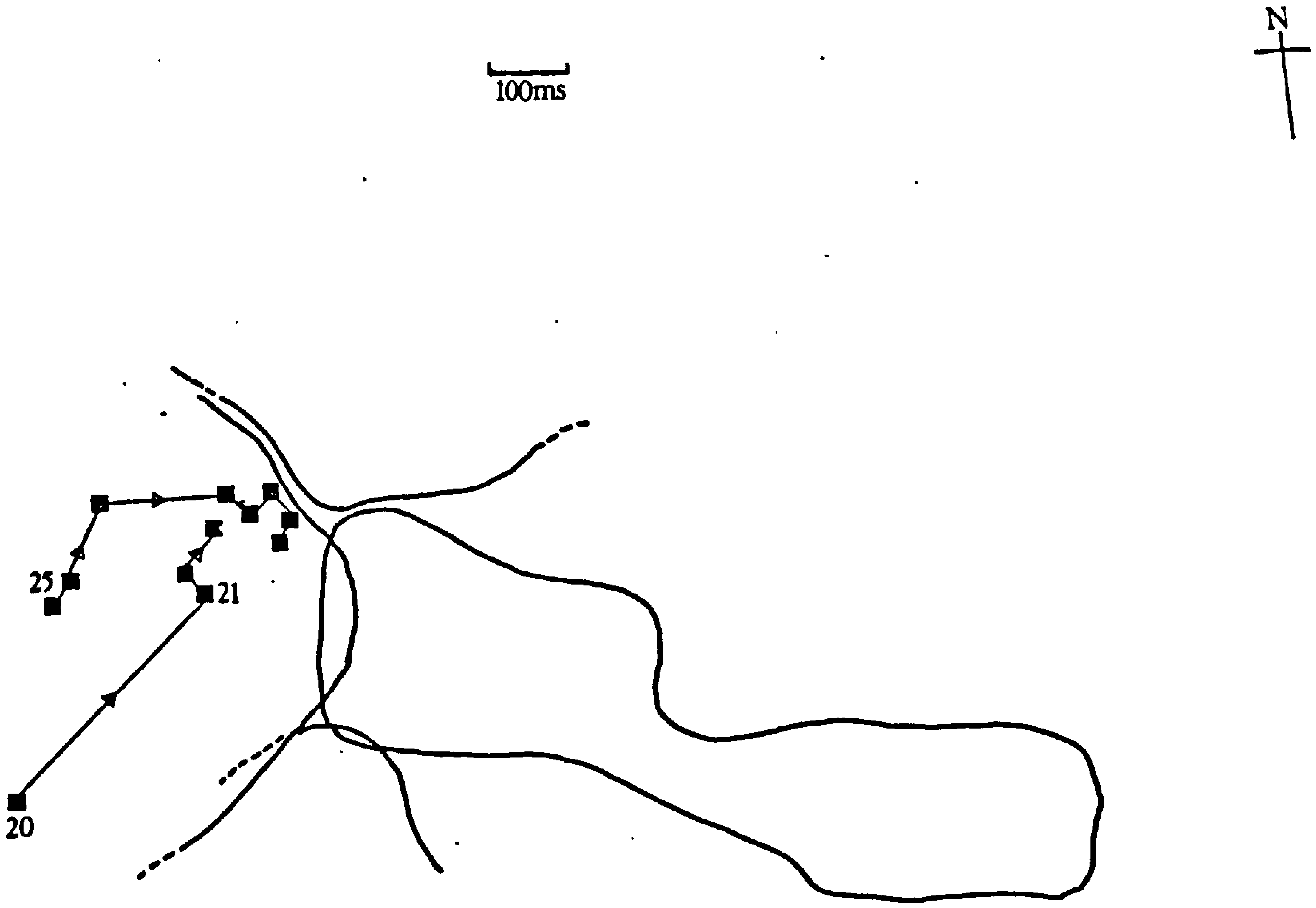
6.7. Non-territorial ranging.

During the month of September 1972, one individual *Indri* ranged over the territories of 2 or 3 groups adjacent to Group V. This animal's characteristic calls enabled plots to be made of its positions whilst Group V was under study (Fig. 7.18). From the structure of the calls (see Chapter 9) the animal was probably male, and was known to range alone as it was found by chance during a nocturnal survey, sleeping alone near the ranging limits of 3 *Indri* groups.

Figure 7.18 Movements of a single *Indri* during the months of September and October 1972. Each spot represents the region of issue of this individual's characteristic "lone" calls.



SEPTEMBER



OCTOBER

Calls from the same individual in October 1972 showed that it had probably restricted its ranging to one territory, part of whose limits had been previously established by another group.

The non-territorial pattern of movements by this individual, which eventually moved away from the area (or changed its vocal characteristics), preceded the mating season by one or two months, and may therefore have been concerned with the acquisition of a mating partner.

7. DISCUSSION

7.1. Ranging by Indri at Analamazoatra.

It is probable that *Indri* normally move about their home ranges only in order to feed. The distance travelled hourly did not differ between groups or across Circuits and the overall seasonal variation in distance ranged appeared, like feeding, to depend mostly on the duration of the activity period. Day to day variability within Circuits was not marked for either group. The two study groups were also similar in their tendency to stay more in some parts of their home ranges than others. By comparing the variability within and between Circuits it is clear that observation periods were too short to accurately examine seasonal changes in home range use.

Two main differences were encountered between the two groups in the way they used their ranging areas:

(a) the tendency by Group V to use some quadrats intensively was distributed equally throughout the year, whereas for Group P it was confined more to certain times, and,

(b) although for Group P the time spent in a quadrat each time it was entered was independent of the total time spent in that quadrat, Group V spent less time per entry in little used quadrats than in heavily used quadrats.

It has been previously suggested (Chapter 6) that food availability may have differed in the two groups according to Group V's poorer knowledge of food location. From the results presented in this Chapter, this view is supported by:

(i) From difference (b), above, Group V may have been ranging so as to acquire knowledge of food location, but returning more rapidly to parts they knew contained food. Group P, however, who spent the same amount of time in a quadrat each time it was entered, appeared to enter each quadrat in order to feed on items they knew existed there.

(ii) The rate of quadrat revisitation was slightly greater in Group V than in Group P, and the percentage of time spent in top ranking quadrats was also slightly greater in Group V.

(iii) The rate and variability with which new quadrats were entered was greater in Group V than in Group P.

(iv) There was more movement within quadrats by Group V than Group P.

(v) There were probably more angled turns executed by Group V than Group P, and angled turns were related to feeding behaviour in the former group.

The fact that these differences were not more marked and that both groups fed for the same proportion of time in parts rarely visited as they did in parts frequently visited either weighs against the hypothesis or suggests that the different strategies adopted by the 2 groups were equally successful.

7.2. Ranging by Primates.

There have been few studies on the ranging behaviour of arboreal primates. This has at least partly been because of difficulties in determining path direction and length due to excessive group dispersion. Some observers for example, have had to adopt average measures for the position of a group by using concepts such as 'centre of mass'(Waser & Floody 1974) whereas others have measured ranging by recording the occupation of home-range divisions large enough to normally contain a whole group (Clutton-Brock, 1972; this study).

Inter-specific comparisons of ranging behaviour are hampered by the use of different observers. These have included daily path length, travel distance, maximum distance reached from the previous night's sleeping site and night position shifts.

For most primate species the distance and direction of movements is related to the dispersion of food. Seasonal changes in the dispersion of food trees resulting from the trees' changing phenology was thought to account for variation in ranging by Colobus badius at Gombe Stream Reserve (Clutton Brock 1975). In the Kibale forest in Uganda, however, the same species living in smaller home ranges apparently responded more to encounters with neighbouring groups than to food location (Struhsaker 1974). The presence of conspecifics, usually advertised by loud calls, is known to influence the movements of gibbons (Ellefson 1968,1974), howler monkeys (Chivers 1969) and mangebeys (Waser 1975), but this influence on ranging has not been demonstrated for all primates which emit these calls e.g. Symphalangus syndactylus (Chivers 1974) and Indri (this study).

The variability in daily ranging distance within species is sometimes enormous. Erythrocebus patas may move as little as 700 or as much as 12,000 metres daily (Hall 1965) and siamang range from 320 to 2,860 metres each day (Chivers 1974). Considering only those arboreal folivore/frugivore species which live in comparably sized areas does not necessarily diminish this variation. The ranges of Alouatta palliata (12 hectares), Presbytis cristatus (20 ha), Symphalangus syndactylus (23 ha) and Indri indri (18 ha) are traversed daily by movements of between 200 and 1000 metres (Chivers 1969,1974; Bernstein 1968).

Primates are clearly very adaptable in the distances they are able to move each day. Despite the fact that those primates with the largest ranging areas (Erythrocebus patas, Theropithecus gelada and Papio sp.) move the furthest, no general relationship can be proposed between range area and daily travel distance for species within major ecological divisions such as 'terrestrial omnivore' or 'diurnal, arboreal folivore' etc. (see Jolly 1972 a).

7.3. Lemur ranging behaviour.

7.3.1. A comparison of Propithecus and Indri ranging behaviour.

In both Indri and Propithecus verreauxi ranging behaviour is characterised by a small day-to-day variability and large seasonal difference in the distance travelled (Richard 1973). For both species those parts of the year when the study groups moved furthest were also the time when they were active longest.

The actual distances moved by the two species, however, differed extensively. Propithecus verreauxi occupied home ranges one half the size of Indri home ranges, but moved each day about twice as far.

From Richard's data it is possible to estimate the mean distance travelled by Propithecus in order to enter a new quadrat in the same way as calculated for Indri in Section 5.4. The observed Propithecus travel distance between quadrats (of 56.4 ms) corresponds closely to the theoretical minimum value of 54.1 ms discussed previously. This suggests that little movement within quadrats occurred, as was observed for Indri Group P. If the southern and northern Propithecus verreauxi study groups are considered separately, it is discovered that the northern groups travelled significantly greater distances in order to enter a quadrat than the southern groups (Mann-Whitney U test, $U=24$; $n_1=n_2=12$; $p(2 \text{ tailed})<0.02$), although there were no differences between groups within each area (Mann-Whitney tests: North $p>0.531$, South $p>0.155$). The northern groups, therefore, not only travelled more between quadrats than the southern groups (Richard 1973) but also moved more within them. This was probably not due to circularity of movement, as the proportion of entered quadrats which had been previously entered did not differ between the two areas. Although vegetation was denser and more diverse in the north compared to the south, the proportion of tree species consumed in the north was less than the proportion of tree species consumed in the south. Species selectivity was therefore greater in the northern study groups. It is possible, therefore, that the northern groups may have had to make more local movements than the southern groups in order to find the right food.

There was no evidence that Indri in Group V varied their diet more than those in Group P. However, the investigatory pattern of travel proposed for Group V from the high rate of local movements, may be considered as food searching, foraging, or selective feeding in the same way that northern groups of Propithecus verreauxi differed from those of the south.

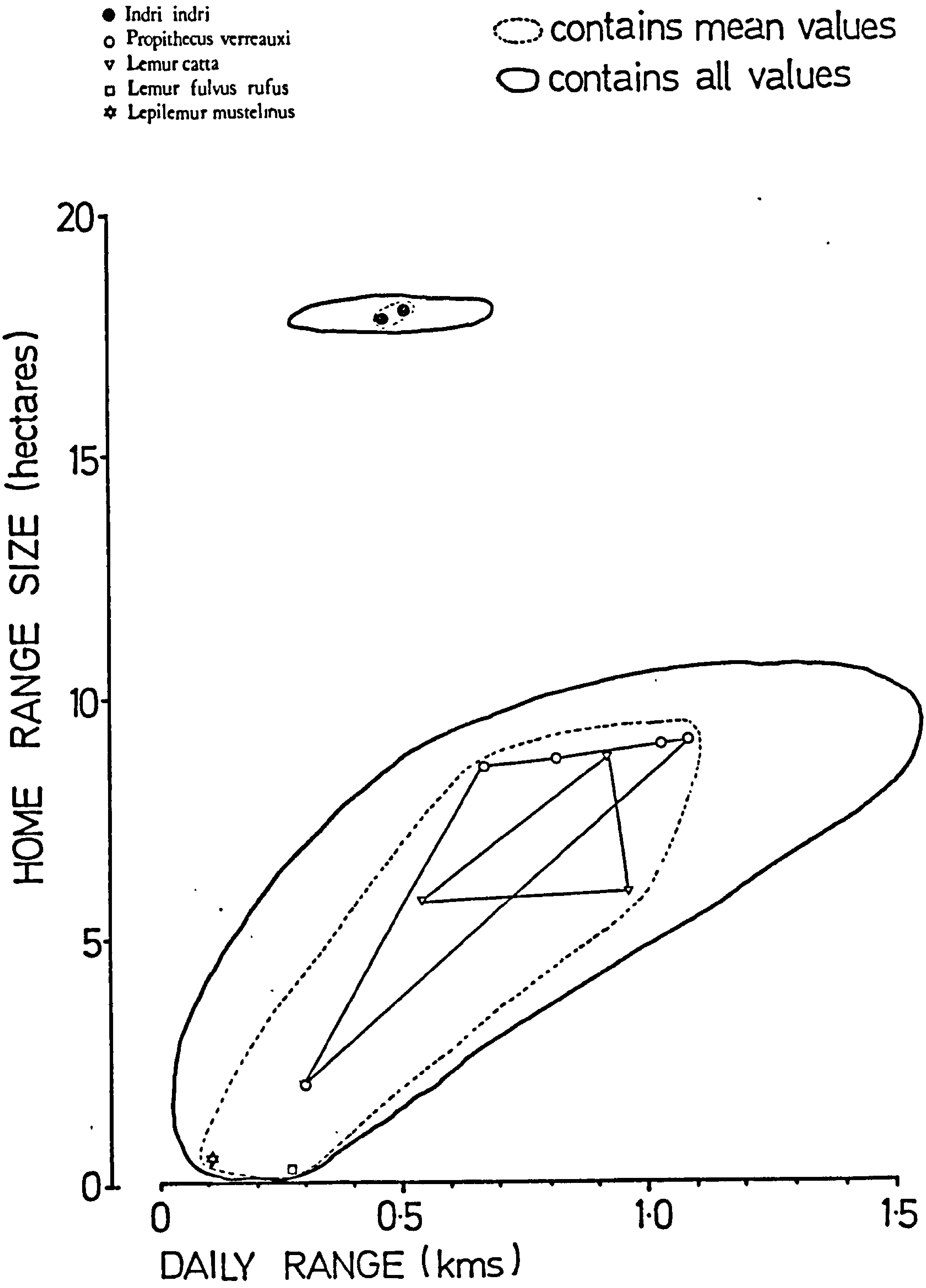
7.3.2. Relationship between ranging distance and home range size in lemurs.

Intra-specific variation in daily ranging distance by the two species most studied, Propithecus verreauxi (Jolly 1966,1972b; Richard 1973,1974b), and Lemur catta (Jolly 1966,1972b; Sussman 1972,1974) is great. Those species studied in the southern gallery forests or Didierea bush nevertheless exhibit fairly consistent relationships between the daily travel distance and home range size (Fig. 7.19). Indri may depart from this pattern, seeming to move relatively less than species inhabiting deciduous forest environments for the same home range size. If this difference is significant it is likely to reflect differences in the dispersion of food about the two main phytogeographic zones as the patterns of movements in those species represented in Fig. 7.19 appear to be related mostly to the dispersion and distribution of food.

7.3.3. Non-nutritive factors influencing ranging by lemurs.

Although some degree of exclusive use of an area is widespread in the Lemuroidea, separate Lemur catta ranging parties at Berenty have been observed using the same food sources at different times on a 'time sharing' basis (Jolly 1972b). There have been frequent reports of lemurs engaging in group encounters, sometimes in areas bordering those which are known to be 'exclusive' and actively defended e.g. Phaner furcifer Propithecus verreauxi, Indri

Figure 7.19 Home range size and daily travel distance in lemurs according to Jolly 1966, Richard 1973, Sussman 1972, Charles-Dominique & Hladik 1971, this study.


● Indri indri
○ Propithecus verreauxi
▽ Lemur catta
□ Lemur fulvus rufus
✡ Lepilemur mustelinus
contains mean values
contains all values
HOME RANGE SIZE (hectares)
20
15
10
5
0
0
0·5
1·0
1·5
DAILY RANGE (kms)

indri. Only in one case, where a group of _P.verreauxi_ spent more time in a border area during a time of the year when group confrontations were frequent, is there any support for a close relationship between territorial defence and ranging behaviour.

Imperfect thermoregulation in lemurs (Chapter 3) could put constraints on ranging activities which are mediated through the need for sleeping associations (_Microcebus_, _L.m.macaco_, _L.m.rufus_, _P.verreauxi_), sunning behaviour (_P.verreauxi_, _L.catta_), and nests or holes (_Microcebus_, _Cheirogaleus_, _Lepilemur_, _Phaner_, _Daubentonia_). Nests and holes may be protective rather than insulatory, but nests, if they take considerable time to construct, or holes, if they take time to find, may be repeatedly used and thus limit ranging in certain ways. _D.madagascariensis_, for example, was observed by Petter & Peyrieras (1970b) to spend about one hour constructing a nest and these authors claim that old nests are repeatedly used.

8. SUMMARY

1. The 'vertical clinging and leaping' locomotion performed by _Indri_ is well adapted to both moving and feeding in the rain forest environment.
2. Neither of the two main study groups spent equal amounts of time in each part of their home range over the year's observations. Differences between Circuits in the amount of time spent in each part of the home range could not be elucidated as each period of observations and the daily ranging distance were too

short. The time spent in a quadrat each time it was entered was independent of the total amount of time spent in that quadrat for Group P but varied for Group V. Group V spent less time per entry in quadrats used little overall than in heavily used quadrats. The proportion of time spent feeding in a quadrat was independent of the amount of time spent in the quadrat for both groups.

3. Sleeping sites appeared to abundant for Indri and the situation of sleeping sites did not apparently influence ranging activities.

4. Group V moved considerably more within quadrats than Group P although the numbers of quadrats entered daily did not differ between groups. Differences between groups in local movements could be attributed to movements between rather than within trees.

5. The two distinct patterns of ranging could be attributed to the absence or presence and distribution of a small number of dense food sources. For most of the year the parts ranged in one day were independent of the parts ranged in the previous day.

6. Differences between the two study groups in the frequency of local movement, the time spent in quadrats once they were entered, the tendency to return to quadrats which had already been entered, and the correlation between movement angles and feeding behaviour, could be accounted for by different properties of the home ranges or by the groups' different

knowledge of the distribution of resources in their home ranges.

7. Ranging distance and direction were not affected by most changes in the weather or by the location of neighbouring groups.

8. Great variability exists in the daily distance moved by primate species with similar habits and similarly sized home ranges. Compared with *Propithecus verreauxi*, *Indri* travel much less despite occupying much larger ranges. This difference may be related to food searching behaviour and the different distributions of food in deciduous and evergreen forests.

CHAPTER 8

Social Behaviour

1. INTRODUCTION

In previous chapters the nature of social influences on individuals' activities and positions have been mentioned where these were relevant and evident. In the following discussion more conventional social characteristics of individuals and groups are described: the dispersion of group members, the distances between individuals and the repertoire and frequency of direct forms of social communication..

Measures of spatial affinity deriving from three sources are contrasted and compared below. Firstly, the tendency for 2 individuals to be seen by the observer at the same time are related to the mean distance separating those individuals. Differences between these 2 measures reflect the tendency for 2 animals to be both not more than and not less than certain distances from each other. For example, 2 animals (A and B) which are often seen simultaneously may not be seen as close together as, say, B and C which are less often seen simultaneously. It is likely in this case that B and C tend to be very close together when they are at all near each other, suggesting that they may be approaching each other in order to engage in social interactions. In contrast A and B may be remaining fairly near each other whilst avoiding direct contact.

Secondly, these two measures of spatial affinity may be related to a random model of intra-group dispersion in order to see how closely this is approximated. In this case the frequency with which each individual is seen by the observer is considered to be independent of the frequency with which any other individual in the same group is seen. If individuals in a group moved randomly with respect to each other the probability of observing two individuals at the same time, $\frac{AB}{P}$, is equal to the product of the probabilities of observing either one:

$$\frac{AB}{P} = \frac{A}{P} \cdot \frac{B}{P}$$

A close fit to this model would be consistent with the view that individuals in the group were behaving similarly not through social communication but because they had similar motivations at the same time. It is worth examining this possibility because further analysis of individuals' spatial relationships would be meaningless unless individuals could be shown to change their relative positions in the group according to other group members' movements.

The aims of the following discussion are to distinguish different social relationships within the study groups using a multifactorial approach - contrasting and comparing the types and frequencies of spatial association and social interaction between pairs of individuals. An attempt is subsequently made to correlate different measures of social interaction in order to test their concordance and to pursue areas of discordance.

2. THE DISTANCES BETWEEN INDIVIDUALS

2.1. Animal associations.

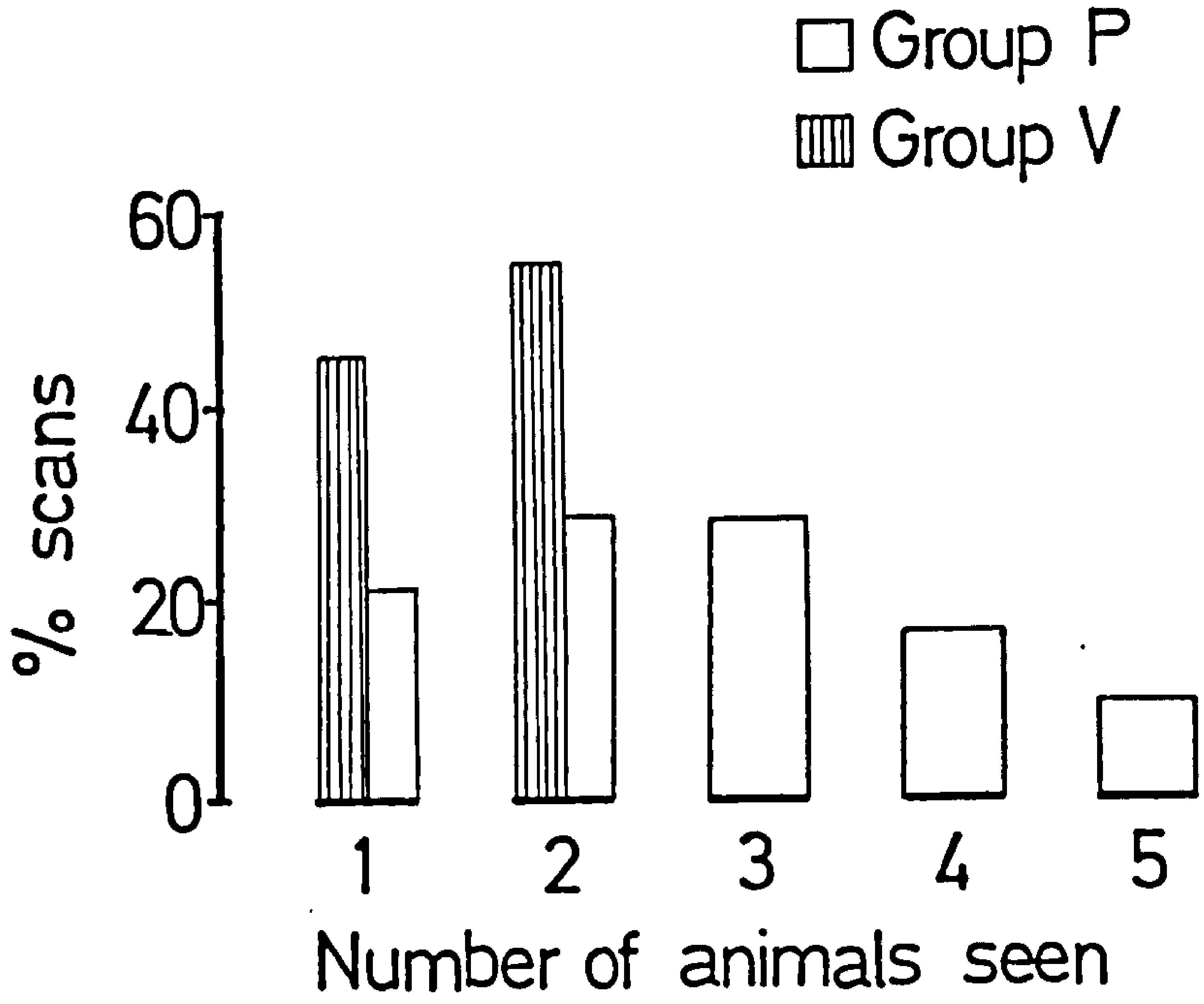
2.1.1. The numbers of animals seen during each scan.

The numbers of animals seen during each visual sweep of the group ("scan") provides a crude measure of group dispersion. The following results often exclude data from Circuit I and, for Group P, Circuit IV. In Circuit I the ability to locate animals was poor and the number of scans in which most members of the group were seen was few. In Circuit IV, the adult female of Group P was unable to move with the rest of the group as a result of a severe wound and this influenced the numbers of animals seen in each scan

Over the whole period of observations the average number of animals seen per scan was 2.3 animals or 47% of Group P and (considering only the two adults) 1.4 animals or 71% of Group V (Fig. 8.1). In Group P, the numbers of animals seen per scan are not distributed about a Poisson curve as individuals, rather than associating randomly (see below), were aggregating at large food sources, defaecation sites and when feeding on earth.

The mean number of animals seen in each scan did not vary seasonally for either Group P or Group V (Fig. 2.5) Seasonal variation in the proportion of scans in which different numbers of animals were seen was, in some cases significant (Fig. 2.5). In Group P, for example, the number of scans in which no animals were seen declined

<u>Figure 8.1</u> The numbers of animals seen in each scan of Group P and Group V over the whole year.


☐ Group P
▥ Group V
% scans
60
40
20
0
1
2
3
4
5
Number of animals seen

steadily over the year - probably more as a result of the observer's improving abilities to locate animals in the foliage than changes in the behaviour of the animals themselves. A gradual increase in the proportions of scans in which one animal was seen probably resulted from this and these two measures were significantly correlated (r^s=-0.76, n=8; $0.01<p<0.05$). No other correlations between seasonal variation in the numbers of scans in which different numbers of animals were seen were significant for this group. In Group V the yearly distribution of scans in which one animal was seen was negatively correlated with the yearly distribution of scans in which both animals were seen (r^s=0.889, n=8; $0.001<p<0.01$), but not with the proportion of scans in which no animals were seen. This suggested that there were differences in group dispersion between Circuits rather than an overall change in the observer's perceptive abilities.

To test whether seasonal fluctuation in the proportion of scans containing each number of animals ("scan complement") was due to the chance effects of sampling, each scan complement for each Circuit was compared to totals composed of all other Circuits together. For Group P, only scans in which 4 animals were seen showed a significant frequency variability over the year (Fig. 2.5); 4-animal scans occurred relatively rarely during Circuits V and VII and frequently during Circuit VIII. In Group V differences were more widespread, a reduction in the proportion of the time that both adults were simultaneously seen during Circuits V and VI being particularly evident.

2.1.2. Individual variation in the proportion of time individuals were seen alone.

The number of times that each individual was seen by the observer when no others were seen simultaneously ("alone") was compared within each group. In Group P (Table 8.1) the oldest offspring was encountered significantly more frequently 'alone' than expected by chance ($X^2_{1df} = 8.9$; $0.001<p<0.01$) and the youngest offspring was seen less often 'alone' than expected ($X^2_{1df} = 9.5$; $0.001<p<0.01$).

No individuals in Group P fed more or less frequently when seen 'alone' than they did overall.

As the adult female of Group V was preferentially followed by the observer, the proportion of observations of her 'alone' was greater (33.6%) than those of the adult male (24.4%). The adult male fed significantly less when seen alone than she did overall ($X^2_{1df} = 7.32$; $0.001<p<0.01$) whilst the male fed equally in these two situations ($X^2_{1df} = 1.3844$; $0.2<p<0.3$).

2.1.3. The frequency with which two animals were seen together.

When any 2 animals in Group P were observed in the same scan they were said to be in each other's presence. The relative frequencies with which any two animals were seen at the same time were considered (i) where there

Group P:

	Ad♀	Ad♂	03	02	01	Total
	51	63	80	59	34	287
	0.71	0.55	8.9	0.04	9.5	X^2 (1df)
>	0.5	0.3	0.001	0.7	0.001	p
<	0.7	0.5	0.01	0.8	0.01	

TABLE 8.1. Individual variation in the amount of time each animal was seen that no other animals were simultaneously seen.

	Ad♂	03	02	01
Ad♀	53,(233)	50,(241)	31,(239)	94,(314)
	Ad♂	26,(185)	39,(211)	42,(262)
		03	64,(207)	37,(239)
			02	48,(238)

TABLE 8.2. Numbers of isolated and inclusive ( ) dyads observed Group P. All year. 15' points.

were no other animals present ("isolated dyadic associations"), and (ii) irrespective of the presence or absence of other individuals ("total dyadic associations").

'Isolated dyadic associations', where two individuals were likely to be separated from others by some distance, were notably frequent for the adult female with O1 (mother and juvenile), and O3 with O2 (the two oldest offspring) and infrequent for the adult male with O3 (Table 8.3)

Measures of 'total dyadic association' firstly revealed general differences in sociability - the adult male being less often observed in the presence of any other individual than both the adult female ($X^2_{1df} = 5.98$; $0.01<p<0.05$) and O1 ($X^2_{1df} = 5.349$; $0.01<p<0.05$) - and secondly exposed differences in the tendency to associate with specific individuals when others were or were not present (Table 8.2). There were three significant differences in this tendency:

(i) The adult female was less often seen in the same scan as O1 when other individuals were present than when they were absent ($X^2_{1df} = 12.47$; $p<0.001$).

(ii) This same property of a relationship was found for O2 and O3. These individuals were seen significantly more often together when no others were present than when others were present ($X^2_{1df} = 0.41$; $0.001<p<0.01$).

(iii) The adult female was seen with any other individual significantly more often when more

OBJECT

		Ad♀	Ad♂	03	02	01
SUBJECT	Ad♀	+	6.1	5.7	3.5	10.7
	Ad♂	6.9	+	3.4	5.1	5.5
	03	6.4	3.4	+	8.4	4.8
	02	4.1	5.1	8.4	+	6.3
	01	11.0	4.9	4.3	5.6	+

TABLE 8.3. Propensity for specific dyadic association (% of subjects' total observations that each other individual was associated with it alone).

Group P:

	Ad♀	Ad♂	03	02	01
n (triads)	194	114	148	128	190
N (total)	878	766	764	760	858
%(of time)	22.1	14.9	19.4	16.6	22.1

TABLE 8.4. The proportion of time spent by each individual in 3-animal associations.

group members were present than when they were absent (X^2_{1df}= 6.35; $0.01<p<0.05$).

2.1.4. The frequency with which three animals were seen together (3-animal associations).

Major differences were found in the proportion of time each member of Group P spent in 3-animal associations (Table 8.4). The adult male was a participant in these associations significantly less often than the adult female (X^2_{1df}= 13.9804; $p<0.001$), O3 (X^2_{1df}= 5.432; $0.01<p<0.05$), and O1 (X^2_{1df}= 7.9433; $0.001<p<0.01$). The sub-adult offspring O2, spent significantly less time in these associations than both the adult female (X^2_{1df}=7.887; $0.001<p<0.01$) and the youngest offspring (X^2_{1df}= 7.94; $0.001<p<0.01$). O2 was seen significantly more often than the adult female in those 3-animal associations where all individuals were in the same tree (X^2_{1df}= 5.742; $0.01<p<0.05$). There were no other differences between individuals in their tendencies to participate in groups of 3 in the same tree.

2.1.5. The frequency with which four animals were seen together (4-animal associations).

No differences were found in individuals' participation in 4-animal associations either overall ($X^2_{1df(max)}$=2.003; $0.1<p<0.2$) or when all animals were in the same tree ($X^2_{1df(max)}$= 0.624; $0.3<p<0.5$).

2.1.6. Expected 'association' frequencies between individuals.

From the frequency that each animal was seen overall, it is possible to construct frequencies with which any 2 individuals would be seen simultaneously, assuming that individuals moved randomly with respect to each other. This approach does not require the assumption that the spatial integrity of the group with respect to the environment is in any way random i.e. all animals in a group might move simultaneously from A to B whilst at the same time moving independently with respect to each other.

If the results are presented as a percentage increment over observed 'association' frequencies (Table 8.5), the close spatial relationship between the adult female and the youngest offspring is immediately clear. Two other results are noteworthy:

(i) the high tendency for O3 and O2 to associate, and,

(ii) the low tendency for the adult male and O1 to associate.

2.1.7. Summary.

(i) Although the mean numbers of animals seen during each scan did not vary between Circuits, distributions of each number of animals seen per scan did. For Group P this appeared to be associated with a better ability to see animals as the study progressed, but for Group V, which were more variable in this measure, differences

	Ad♂	03	02	01
Ad♀	27.6	26.3	16.3	102.5
Ad♂		21.3	41.2	8.3
03			63.4	37.4
02				36.7

TABLE 8.5. The degree to which each 2 individuals associated together more than randomly (presented as a % of expected values if individuals had associated randomly).

Metres:	0-3	4-13	14+	%	Total n
Ad ♀	30.7	49.2	20.1	100	1255
Ad ♂	24.8	52.3	22.8	100	1051
03	24.2	55.6	20.2	100	1049
02	30.8	51.8	17.4	100	1080
01	37.2	48.2	14.6	100	1277

TABLE 8.6. Mean categorised distances separating each individual from any other individual (presented as percentage of an individual's IIDs per category).

	Ad ♂	03	02	01
Ad ♀	9.7**	11.9***	0.01	12.6***
	Ad ♂	0.1	9.5**	40.8***
		03	11.7***	45.1***
			02	10.5***

(1) 0-3 metres

	Ad ♂	03	02	01
Ad ♀	2.2	9.2**	1.5	0.26
	Ad ♂	2.2	0.07	3.86**
		03	3.12	12.42***
			02	2.90

(2) 4-13 metres

	Ad ♂	03	02	01
Ad ♀	2.59	0.01	2.71	13.45***
	Ad ♂	2.14	9.78**	26.37***
		03	2.74	12.94***
			02	3.54

(3) 14+ metres

TABLE 8.6a. Differences in the above measure (X^2_{1df} values for each indivdidual tried against every other individual for each category).

* p<0.05

** p<0.01

*** p<0.001

probably reflected changes in intra-group animal dispersion.

(ii) Within Group P the oldest offspring was seen alone more often than expected by chance and the youngest offspring was seen alone less often than expected by chance. The adult female of Group V was the only individual whose tendency to feed differed when seen in the absence or in the presence of another individual.

(iii) The adult male of Group P was less often seen with at least one other group member nearby than the adult female and youngest offspring. With 2 exceptions different pairs of animals were similar in their tendencies to be together when no other animals were present: the adult female and 01 were relatively often seen together, as were 03 and 02. Both these pairs associated more frequently in the absence than in the presence of others, whereas the adult female associated with 02 more often when other group members were near.

(iv) The adult male and 02 individuals participated less often than others in 3-animal aggregations.

(v) Animal pairs associated more often than expected on a 'random movement' model by a mean of 38.1%. Only 3 animal pairs exceeded this mean: Adult female with 01, 03 with 02, and Adult male with 02.

2.2. The distances between individuals.

The preferences for general and specific social environments exhibited by each individual were elucidated in two ways. Firstly, the overall or average distances maintained by individuals from any other group member were calculated. Secondly, spatial measurements were attributed to specific relationships. Where possible, the synchrony and asynchrony of activity of different animal pairs were compared between conditions of differing spatial proximity.

2.2.1. Group P.

Three inter-individual distance (IID) categories were defined: 0-3 metres, 4-13 metres and 14+ metres (Table 8.6). Differences between individuals' tendencies to remain close to or far from all other group members were then compared. The greatest number of significant differences (8) were found in the proportions of time individuals spent very close to others i.e. in Category 1 (0-3 metres), and fewest differences were found (3) in intermediary spatial preferences, Category 2 (4-13 metres):

Category 1. The youngest individual O1, stayed significantly closer to others than any other group member. The oldest offspring, O3, was less often seen closer to any group member than any other individual except the adult male.

Category 2. The adult female and the youngest offspring spent more time than the older offspring at these distances (4-13 ms) from others. In addition, the O1 individual spent more time in this category than the adult male.

Category 3. As expected, O1 spent less time over 14 metres from others than all other group members except

02. The adult male spent more time in this category than 02.

Measures of mean distance between each individual and every other group member satisfactorily summarize these results (Table 8.7), but as the observer could rarely see animals more than 60 feet apart, these distances indicate no more than relative characteristics of spatial arrangement within Group P.

Differences in the categorised distances between every 2 individuals in the group were examined (Table 8.7). The spatial relationships between the adult female and 01, and 02 and 01 were found to be much closer than any others by this measure. Other differences may be discussed by referring to the relationships held by each group member separately:

(a) Adult female. The relationship between the adult female and 01 was significantly closer than all others in the group.

(b) Adult male. The relationships of the adult male with both 01 and 02 were significantly closer than those with the adult female or 03 individuals.

(c) 03. The relationship 03 maintained with 01 was significantly closer than the relationship with the adult male.

(d) 02. 02's spatial relationship with 01 was significantly closer than all his other relationships.

(e) 01. All relationships except that between 01/adult male and 01/03 were significantly different.

No	Relationship	0-3 ms	4-13 ms	14+ ms	Total	Mean distance
1	Ad♀ - Ad♂	59 (20.6%)	146	81	286	6.9
2	- 03	59 (20.3%)	169	63	291	5.5
3	- 02	71 (26.3%)	138	61	270	3.8
4	- 01	196 (48.1%)	165	47	408	3.8
5	Ad♂ - 03	41 (19.4%)	118	52	211	6.4
6	- 02	73 (29.2%)	132	45	250	5.3
7	- 01	88 (29.0%)	154	62	304	4.2
8	03 - 02	76 (27.9%)	144	51	271	5.5
9	- 01	78 (28.3%)	152	46	276	5.4
10	02 - 01	113 (39.2%)	145	31	289	4.2

TABLE 8.7. Inter-individual distances in Group P (% in brackets).

	2	3	4	5	6	7	8	9	10
1	3.9	3.69	64.3•••	1.2	10.1••	7.9•	8.6•	12.2••	39.3•••
2		3.5	58.0•••	0.6	5.96	16.0•••	4.7	5.8	29.7•••
3			36.1•••	3.1	1.8	0.7	1.2	3.0	18.9•••
4				52.0•••	23.4•••	28.9•••	28.0•••	26.9•••	6.7•
5					7.0•	6.2•	5.7	7.6•	30.3•••
6						0.5	0.11	0.3	9.0•
7							0.39	1.64	13.3••
8								0.45	11.56••
9									10.85••

• $p<0.05$
•• $p<0.01$
••• $p<0.001$

Comparison of relationships for 3 categories by X^2_{2df} test. (X^2_{2df} values presented).

Too few records of IID were obtained to allow examination of seasonal variation in social distance.

It might be reasonably expected that the number of times 2 individuals were seen in the same group scan would be a function of the distance normally separating them. Although the observed frequency that each pair of individuals in Group P were seen together was correlated with the mean IID (2 tests: $r^s_{(observed)} = 0.174$; $r^s_{(theoretical)}$[1]$= 0.17$). The tendency for animals to be seen together, therefore, did not define the distance they remained apart. There was no reason to believe that different individuals could be recognised differently at various distances, and it seems plausible to suggest, therefore, that some animals when they approached others, either came as near as possible, or, remained beyond a critical but viewable distance (probably less than 20 metres). This view is supported by Table 8.6 where differences between individuals' IID relationships appear to be diluted with distance. Most differences are manifested in close associations (Category 1) and few in situations where animals were farther apart (Categories 2 and 3).

2.2.2. Group V.

Because adults of Group V rarely came within 3 metres of each other, different inter-adult distance categories from those used for Group P (above) were defined in order to examine seasonal variation of this measure (Fig. 8.2).

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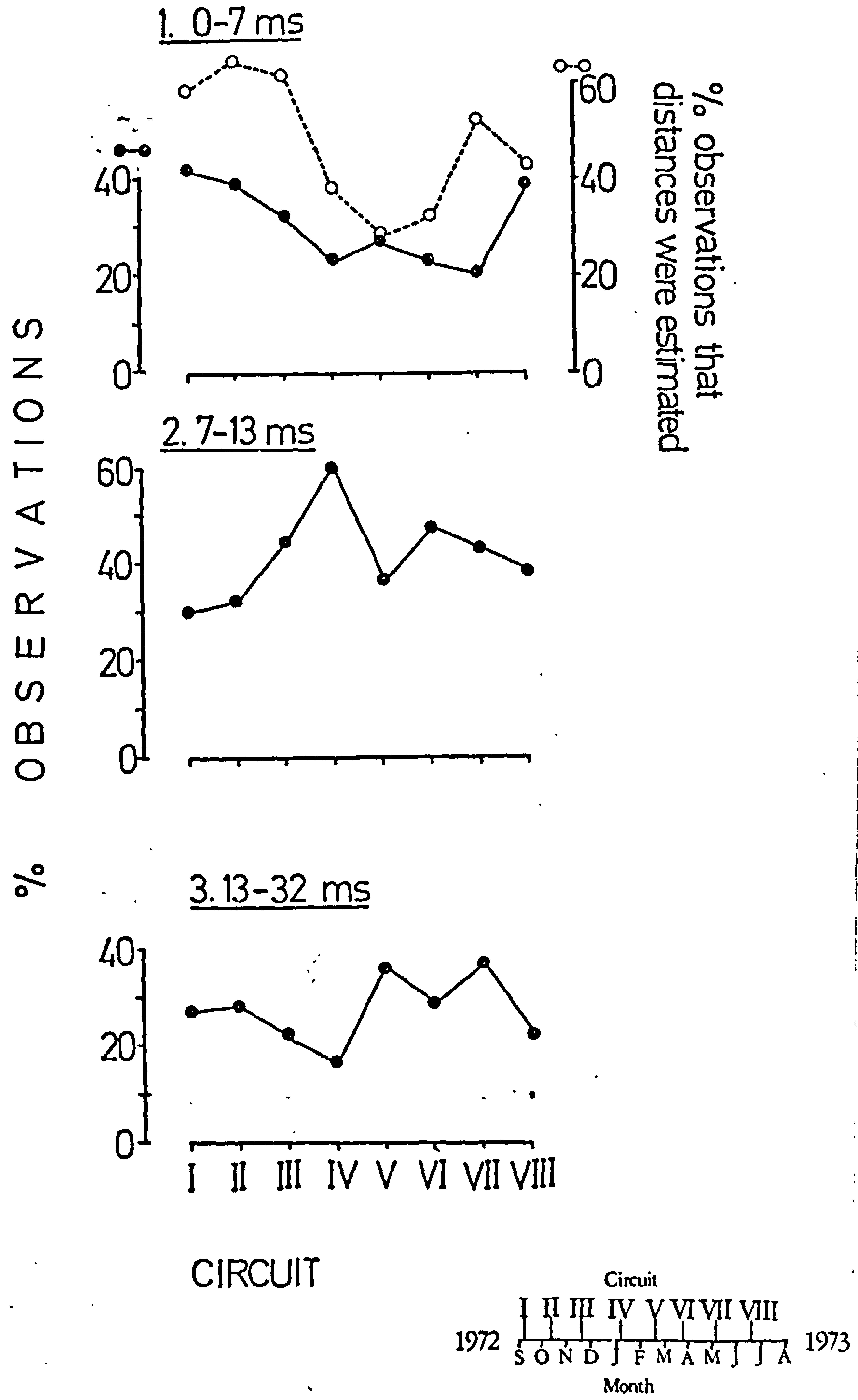
[1] based on expected associations according to the 'random movement model'

Figure 8.2 Seasonal variation in the proportions of time the adults of Group V were separated by (1) 0-7 metres, (2) 7-13 metres and (3) 13-32 metres. The % of observations including estimates of distance between adults is also shown.


1. 0-7 ms
2. 7-13 ms
3. 13-32 ms
% OBSERVATIONS
% observations that distances were estimated
0
20
40
60
I
II
III
IV
V
VI
VII
VIII
CIRCUIT
Circuit
1972
1973
S O N D J F M A M J J A
Month

Tests were applied to try seasonal variation in each category's values and these resulted in significance for Category A (0-7 metres), B (7-13 metres) but not for C (13-32 metres). However, the variation between Circuits in the proportion of sampled behaviour that contained IID measurements was also great ($X^2_{7df}=100.32$; $p<0.001$), and these results must be considered in the light of this great observational variability, whose cause is unknown. It was certainly not true, for example, that at the time when fewest IID estimates were obtained the animals were recorded as being furthest apart.

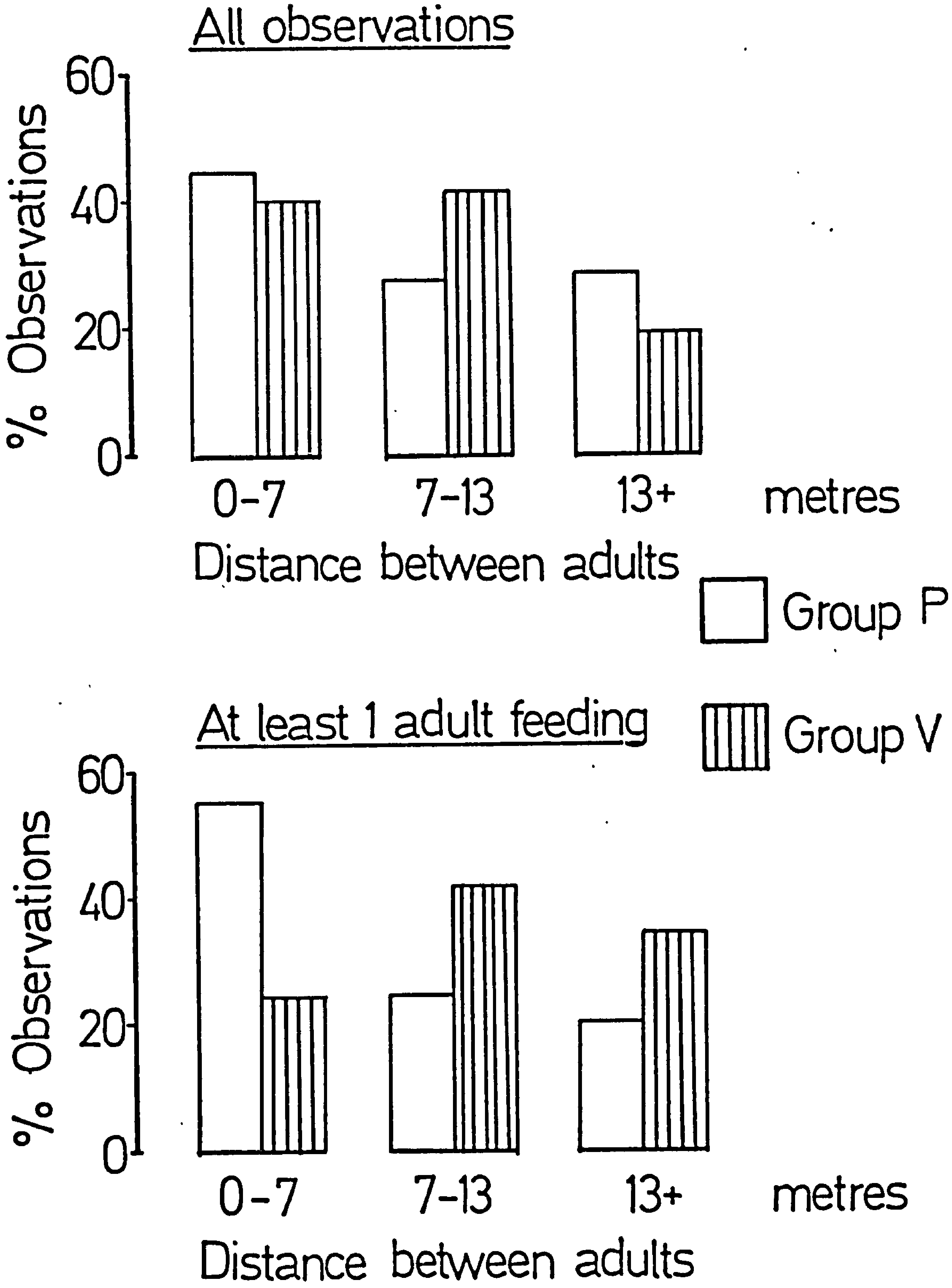
If the distances between adults during each Circuit are compared to their distances during all other Circuits together, significantly greater IID measurements are obtained during Circuit IV ($X^2_{2df}= 10.09$; $0.001<p<0.01$ with Yates' correction for continuity) and Circuit VII ($X^2_{2df}= 7.225$; $0.01<p<0.05$) than for the rest of the year. The reasons for this variation are unknown, but adults were not observed relatively infrequently in the same scan at these times of the year (see Fig. 2.5). It is possible that short term changes in spatial relations within the group occurred with a periodicity that combined unfortunately with the duration of observations each Circuit.

2.2.3. Inter-group adult comparisons.

2.2.3.1. Distance between each group's adults.

The distance between the adults of each group were found to differ considerably (Fig. 8.3), both overall

Figure 8.3 Comparison between groups in the categorised distance separating adults (1) overall, and (2) when at least one of the adults was feeding, for the whole year.


All observations
% Observations
60
40
20
0
0-7
7-13
13+
metres
Distance between adults
Group P
Group V
At least 1 adult feeding
% Observations
60
40
20
0
0-7
7-13
13+
metres
Distance between adults

(X^2_{2df}= 19.08; $p<0.001$) and for situations where at least one of the adult pair was feeding (X^2_{2df}= 62.06; $p<0.001$). Whereas overall IIDs between adults were not clearly related simply to proximity (Fig. 8.3), when feeding the Group P adults stayed much closer to each other than those in Group V . A closer look at the relationship between the adults' activities and IIDs was therefore made.

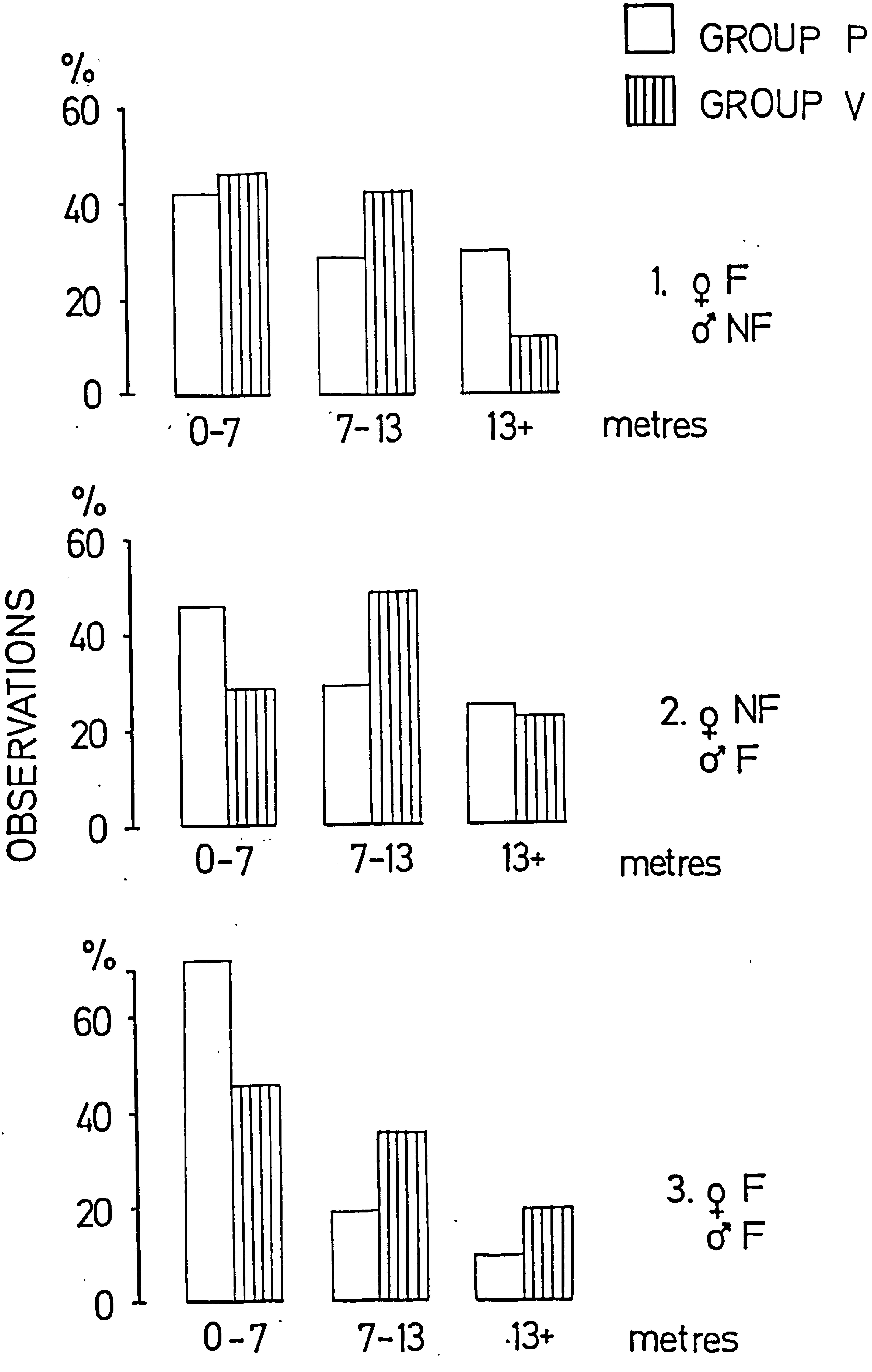
2.2.3.2. Activity synchrony and inter-adult distances within groups.

The distances between adults were computed for situations where (i) the adult female was feeding and the adult male was not feeding; (ii) the adult female was not feeding and the adult male was feeding; (iii) both the adult male and the adult female were feeding.

(a) Group P.

No differences were found between conditions (i) and (ii) above where only one adult was feeding (X^2_{2df}= 0.2115; $0.8<p<0.9$), but there were significant differences between instances when both adults were feeding (adults relatively close together) from when only the adult female was feeding, when adults were relatively far apart (X^2_{2df}= 14.92; $p<0.001$) as illustrated in Fig. 8.4. Small sample sizes prohibited the third test-condition (ii) versus (iii) above-over all categories. In one category, however, there were sufficient sample sizes, and this proved that when both

Figure 8.4 Comparison between groups in the categorised distance separating adults throughout the year for conditions where (1) The adult female was feeding and the adult male was simultaneously not feeding, (2) the adult female was not feeding and the adult male was simultaneously feeding, (3) both adults were simultaneously feeding.


GROUP P
GROUP V
OBSERVATIONS
%
60
40
20
0
0-7
7-13
13+
metres
1. ♀ F
♂ NF
2. ♀ NF
♂ F
3. ♀ F
♂ F

adults fed they were significantly closer than when the adult male only was feeding ($X^2_{1df} = 4.24^*$, $0.01<p<0.05$).

(b) Group V.

Parallel tests were tried for Group V (Fig. 8.4). Over all categories the only significant difference in adult IID occurred between situations where only the adult female was feeding (low IID) and where only the adult male was feeding (high IID; $X^2_{2df} = 9.54$; $0.001<p<0.01$). The distance between adults when they were both feeding did not differ significantly from instances either where the adult female only fed ($X^2_{2df} = 4.24$; $0.1<p<0.2$) or where the adult male only fed ($X^2_{2df} = 5.96$; $0.05<p<0.1$). However, when the adult male only was feeding adults were less often within 6 metres of each other than when both adults were feeding ($X^2_{1df} = 5.76$; $0.01<p<0.05$).

2.2.3.3. Activity synchrony and inter-adult distances between groups.

It is evident that overall differences between groups in adult IID were accentuated and focused into a clear relationship when feeding records only were considered (Fig. 8.4).

When only the adult female in a group was feeding Group P adults were significantly farther apart than Group V adults ($X^2_{2df} = 14.03$; $p<0.001$), and when both adults fed Group P adults were significantly closer than Group V adults ($X^2_{2df} = 13.13$; $p<0.001$). Insufficient sample

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*Yate's correction for continuity applied.

sizes prohibited inter-group adult IID comparisons to be made for conditions where only the adult male in a group was feeding.

In summary, differences between the adults' IIDs in Group V depended on their relative activity, or vice versa. This was not true for Group P. In Group P adults could feed close together, but in Group V they did not. No specific distances could be isolated as of critical importance in these effects, but the greatest intra- and inter-group differences were found in the closest category where adults were separated by a distance of less than 6 metres.

2.2.4. Group dispersion and position in sleeping positions.

Very shortly after the last feeding observations, individual Indri almost simultaneously took up characteristic sleeping positions. The sleeping position could be instantly recognised by its height (see below), the diameter of the support, and the self-grooming or scratching that immediately commenced.

Records of the height of sleeping Indri were made on 134 occasions for Group P and on 50 occasions for Group V. The mean height of sleeping postures (Group P, 20 metres; Group V, 18 metres) contrasted with normal heights during the active period (for both groups 14 metres), and were slightly less variable ($\sigma_{sleep} = 5.6$; $\sigma_{active} = 6.2$ metres).

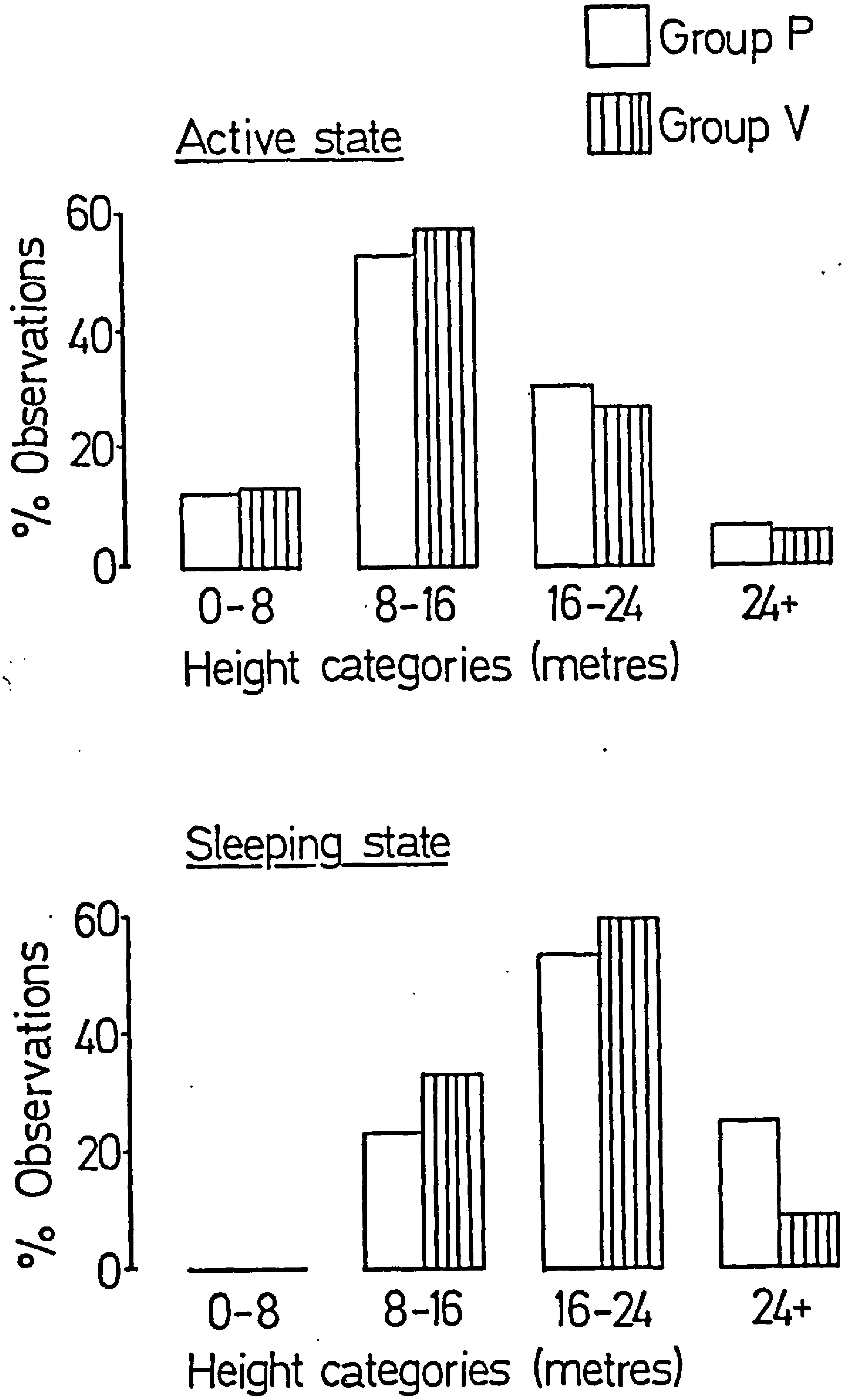
Overall, Indri of Group P spent most of the active period equally in the various canopy levels (see Chapter 5).

They slept, however, predominantly in the 'canopy bottom' and 'middle canopy' parts of the trees ($X^2_{2df} = 24.06$; $p<0.001$), which were reasonably high and offered a variety of wide supports that could be rested upon rather than grasped. No significant differences in canopy utilisation between active and sleeping states were found for Group V ($X^2_{2df} = 2.332$; $0.3<p<0.5$), although sample sizes were small.

Although the mean sleeping height of the two groups was found to be different (Student's 't' = 2.64; $0.001<p<0.01$) so were the variances ($t = 2.3$; $0.01<p<0.05$) and comparisons therefore had to be made through category divisions (Fig. 8.5). Both Group P and Group V slept significantly higher than they fed and rested during the day (2 tests: Group P $X^2_{3df} = 114.99$, $p<0.001$; Group V $X^2_{3df} = 30.29$; $p<0.001$), and although their daily heights were not significantly different ($X^2_{3df} = 6.91$, $0.05<p<0.01$), Group V slept lower than Group P ($X^2_{2df} = 6.24$; $0.02<p<0.05$) at night.

The impression gained by the observer, and supported by these results, was that Group P were more selective and chose specific parts of large trees to sleep in, whilst Group V were more likely to sleep anywhere. It is possible that nocturnal predators were avoided by selecting suitable sleeping locations and this could explain why trees of different heights and different parts of the trees were being used at night, but not the difference between groups. If height in night positions was increased for defensive

Figure 8.5 Comparison between groups in the categorised heights taken by group members in the trees for (a) the activity period, and (b) the sleeping period.



Group P
Group V
Active state
% Observations
60
40
20
0
0-8
8-16
16-24
24+
Height categories (metres)
Sleeping state
% Observations
60
40
20
0
0-8
8-16
16-24
24+
Height categories (metres)

reasons then Group V (with an infant) might have been expected to sleep higher than Group P. They, in fact slept significantly lower. Substantial support diameter was probably a more critical parameter in sleeping site choice for all individuals, and these may well have been better available in tall trees.

The differences between groups is not fully understood. The sleeping positions that Indri took in trees, however, may have been more selective than was apparent to the observer i.e. sleeping sites for some reason may not have been plentiful. If this was the case it is conceivable that Group P were sleeping in carefully chosen places whilst Group V, perhaps unaware of the best sleeping sites, were being less selective.

Very few records of inter-individual distances were obtained when animals were in sleeping positions. The 80 IID records collected of Group P members in sleeping positions were biased towards the relatively rare situation when most or all the animals were visible. 32% of these records described the distance between the adult female and the youngest offspring (O1), animals which slept either together or close to each other. Only 15 sleeping IIDs were recorded in Group V.

Apart from the adult female + infant combination (Plate 3.1) individuals usually slept well dispersed in several trees. In severe weather conditions, the adult male and O2 or O3 and O2 would form a sleeping pair, but this was rarely seen. No more than two animals would ever sleep together.

Normally, the adult female was followed to her sleeping position by the infant or juvenile, but on at least one occasion the adult female of Group V, having already adopted a sleeping position, returned to sleep in a spot where she had previously left the infant. The impression was gained that this female tended to choose hidden sleeping spots in tangles of foliage, making her unobstrusive or difficult to see with the infant.

Hard rain caused Indri to move to firmer rather than sheltered supports, although the latter were plentiful.

2.3. Progression orders.

Indri groups move in an essentially linear fashion through the forest. Although animals may be slightly dispersed perpendicular to the direction of travel, they often take similar or identical paths. Normally, only one individual is moving at any one time and animals frequently overtake other temporarily stationary animals. These characteristics, and the difficulty in pursuing Indri whilst simultaneously recording behaviour, made records of progression order hard to obtain. As their patterns of ranging became better known, however, the observer could predict where the group was going, choose a better route on the ground, and arrive first. In these instances, progression orders could be noted and the results are presented in Table 8.3 Due to the very biased conditions of movement by the observer when watching Group V, data for this group may be rejected as probably inaccurate. There was no consistent leadership by one individual in this group.

		1st	2nd	3rd	4th	5th	Total
GROUP P	Ad♀	6	5	4	4	2	21
	Ad♂	11	1	2	2	5	21
	03	3	5	5	3	8	24
	02	5	9	4	3	1	22
	01	1	5	8	6	2	22
GROUP V	Ad♀	6					
	Ad♂	5					

TABLE 8.8. Progression orders in Groups P and V.

Ad♀	Ad♂	03	02	01	Ad♀	Ad♂ (Inf)
19.1	19.5	9.3	26.7	25.2	38.8	36.7 (24.5)
GROUP P					GROUP V	

TABLE 8.9. ALLOGROOMING - (i) Bout participation.

In Group P the adult male was seen to be first in group progressions considerably more often than in any other position, and O1 considerably less than in any position.

Comparison of progression orders with tree departure orders (Chapter 6) reveals a similar pattern: the adult male almost always left first from trees in which all animals fed, O2 second, and O3 towards the end. Although there were few data to confirm it, this consistency did not extend to a general leadership by the male in all aspects of movement, as he was frequently the last individual to enter large feeding trees as well as being the first to leave them. In Group IV at Vohidrazana, the oldest offspring (an adult-sized female) always entered and departed from feeding trees last. In this group the adult female, which had recently given birth, consistently led the group to new feeding trees.

2.4. Summary.

(i) The juvenile (O1) in Group P was more often observed closer to any other animal in the group than the other group members. The adult male and (especially) O3 were more often observed further from any other animal, than the other group members.

(ii) In spatial terms, the relationship between the adult female and O1 of Group P was the closest, followed by the relationship between O2 and O1 - the youngest offspring. All relationships involving the adult male were relatively distant, as were those involving O3. O2's spatial relationship with O1 was much closer than any of his other relationships. As in (i) above, O1 formed closer or intermediary spatial relationships with all other group members, compared to any other animal. The adult female and adult male kept far apart, as did the adult male and O3. Within the group differences were encountered between pairs of animals in the numbers of times 2 individuals were seen together and the distance they kept apart.

(iii) In Group V both the number of records of distances between adults and the distances themselves varied considerably over the year.

(iv) The distances between adults of each group were different and were dependent on individuals' activities. There were no differences in the distances between Group P adults, whether the adult female only or the adult male only was feeding. In Group V, however, these differences were marked - much greater distances were present if the adult male only was feeding than if the adult female only was feeding. When both adults were feeding, those in Group P were much closer than those in Group V, although when only the adult female of each group was feeding the adults of Group P were much farther apart than those of Group V.

3. THE SOCIAL ACTIVITIES OF INDRI

This section concerns itself with direct, though not necessarily overt, influences exerted on one animal's behaviour by another. Only behavioural interactions normally occurring within groups are described here. Vocalisations and social activities concerning communication between groups are presented in the following chapter.

Activities with social connotations are loosely classified below as 'affiliative' or 'agonistic'. This is a premature and possibly misleading division which implies social function where this can often not be demonstrated. It is also unsatisfactory in that some activities commonly involve, both for <u>Indri</u> and other primates, elements of behaviour which contain both aggressive and relaxed actions. Sexual behaviour and play-wrestling are (perhaps not unrelated) examples of this 'paradox'. The classification is adhered to below by the following definition: "agonistic" interactions involve an aggressive component alone, whereas "affiliative" interactions are distinguished by relaxed (i.e. non-aggressive) contact behaviour for most of their duration, or by tolerance of extreme proximity of other group members.

In this study full sequences of reproductive behaviour were not seen in any <u>Indri</u> group. As the attempted copulations observed were always immediately and aggressively rejected by the adult female concerned, they are placed under the 'agonistic' section below. Further study will, presumably, alter this classification.

3.1. Affiliative interactions.

3.1.1. Allogrooming.

3.1.1.1. Introduction.

Indri groom group members' faces, necks, ears and backs - those body parts that can not be self-groomed. Allogrooming (Plate 8.2) generally follows a 'request' gesture; one animal approaching another (which itself may be sufficient to induce allogrooming), reaching out and touching the potential groomee before starting to allogroom. Allogrooming itself may act as its own invitation - a very short bout by one individual being followed almost immediately by a long bout in the reverse direction.

Unlike other lemurs which may form social chains of simultaneously allogrooming individuals (e.g. *Hapalamur griseus*, *Lemur fulvus*; pers. obs.), in *Indri* only two animals are involved at any one time and if participants reciprocate, they only groom each other alternately, sometimes switching the roles of groomer and groomee several times within one bout.

The action of grooming itself is the same whether the groomer is grooming itself or another individual. The head is moved in vertical stroking movements, forward and up, only the forward movement contacting the recipient whose head is normally held in a firm position by the groomer's arm and hand. Most if not all grooming behaviour involves the use of both tongue and 'tooth-comb' (see Appendix 3) in licking, combing and scraping actions.

Indri spend only small amounts of time grooming or

PLATE 8.2 Allogrooming in *Indri*. The adult female (left) allogrooms the back of the juvenile's neck (Group P).

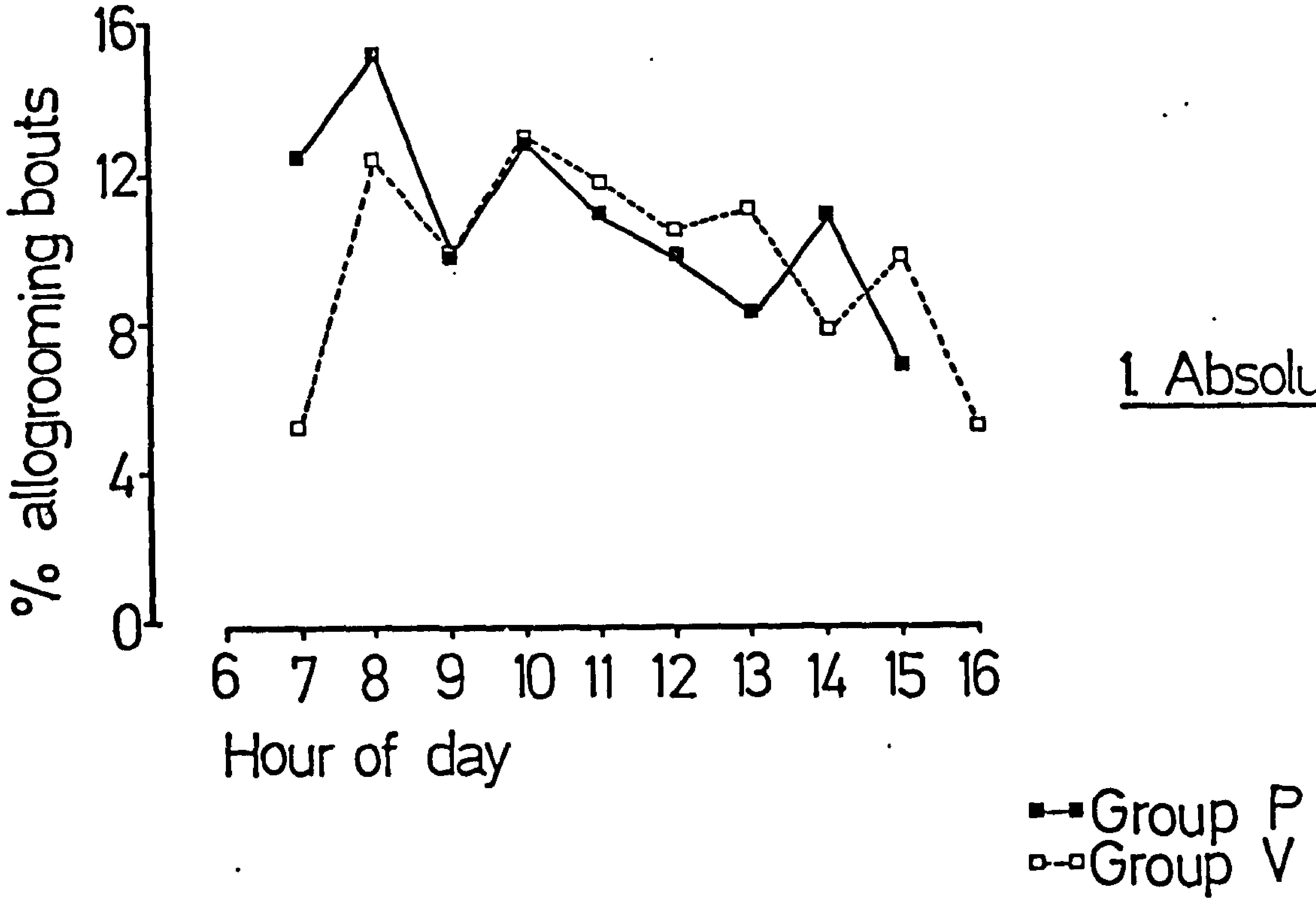
allogrooming. Group P spent 4.0% of their activity period self-grooming and 0.7% allogrooming. Corresponding figures for Group V were 1.5% and 0.4%. In neither group did animals groom more in non-active states (i.e. before and after feeding) than during the active period of the day although allogrooming was often seen just before animals settled into final sleeping positions for the night. There were no clear temporal differences in the hourly distribution of allogrooming (Fig. 8.6), but peaks were apparent for Group P in the first and last parts of the active day.

In Group P there were 262 bouts and in Group V 150 bouts of allogrooming observed over the year. In neither group were frequencies of this behaviour sufficient to permit seasonal comparisons.

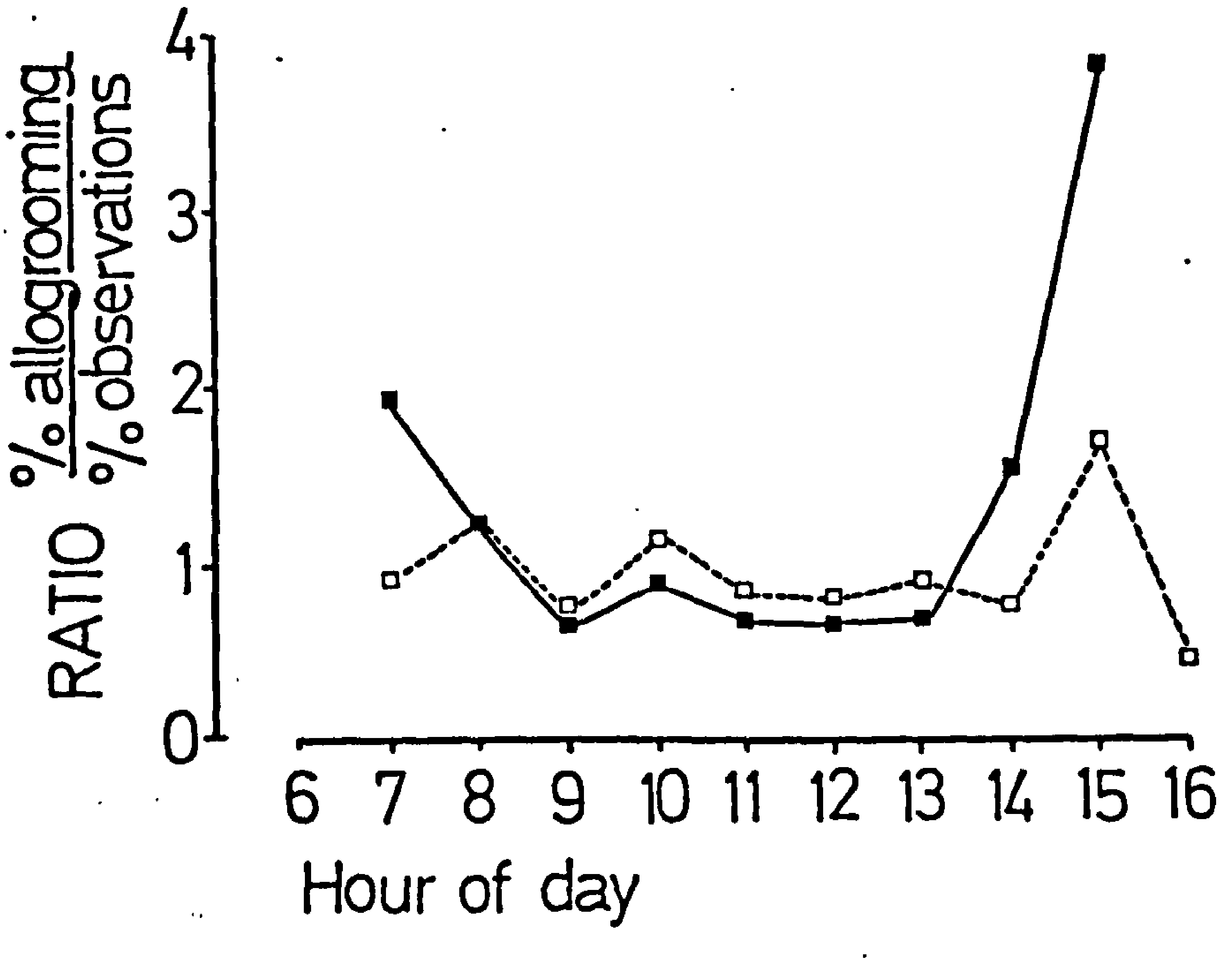
Individual variation in allogrooming participation (Table 8.9) shows that in Group P the most frequent groomers were O2 and the adult male, and the least frequent groomer O3. In being groomed, O1 was the most successful and O3 the least successful. If the proportion of its allogrooming bouts that each individual was <u>groomed</u> is computed, then for each grooming action O2 and the adult male (who groomed the most) were the least successful individuals (in getting groomed) and O1 the most successful (Table 8.10).

In Group V (Table 8.10), the adult male was involved in 37% of observed allogrooming bouts and groomed others in 60.6% of these. The adult female was involved in 39% of the observed allogrooming bouts and groomed

<u>Figure 8.6</u> Hourly distribution of (1) the observed number of allogrooming bouts (Absolute) and (2) the estimated total number of allogrooming bouts (Relative), for Group P and Group V throughout the year.



1. Absolute



2. Relative

GROOMER

GROOMEE

	Ad♀	Ad♂	O3	O2	O1	Total	%
Ad♀	-	3	1	21	32	57	21.8
Ad♂	1	-	3	23	4	32	12.2
O3	0	6	-	21	0	27	10.3
O2	7	25	18	-	3	53	20.2
O1	35	36	0	22	-	93	35.5
Total	43	70	22	87	39	262	
%	16.4	26.7	8.4	33.2	14.9		

Ratio $\frac{\text{GROOMEE}}{\text{GROOMER}}$:

Ad♀	Ad♂	O3	O2	O1
1.3	0.46	1.2	0.61	2.4

(i) GROUP P

	Ad♀	Ad♂	Inf.	Total	%
Ad♀	-	63	20	83	50.3
Ad♂	21	-	0	21	12.7
Inf.	24	37	-	61	37.0
Total	45	100	20	165	
%	27.3	60.6	12.1		

Ratio $\frac{\text{GROOMEE}}{\text{GROOMER}}$:

Ad♀	Ad♂	Infant
1.84	0.21	3.0

(ii) GROUP V

TABLE 8.10. ALLOGROOMING - (ii) Bout direction.

others in 27% of these. As a proportion of the total number of bouts involving each individual, the adult male was groomed for 17.3%, the adult female for 64.8% and the infant for 75.3% of the observations.

3.1.1.2. Specific grooming combinations.

(i) Group P.

Allogrooming combinations which were never or infrequently seen were:

(a) Adult female allogrooming the adult male or O3

(b) Adult male allogrooming the adult female or O3

(c) O3 allogrooming either adult or O1

(d) O1 allogrooming the adult male, O3 or O2.

Only 9 substantial allogrooming relationships were observed:

(a) O2 allogroomed everybody equally, but was only allogroomed by the adult male and O3 animals.

(b) O1 allogroomed only the adult female but was allogroomed by all except O3.

(c) O3 allogroomed only O2 and was only allogroomed by him.

(d) The adult male allogroomed only O2 and O1, but only received grooming from O2.

Both adult male and O3, therefore, were substantially groomed only by O2, which in turn was groomed only by them. The adult female and O1 groomed each other substantially and both received grooming from O2. The adult male groomed O1 but not the adult female.

(ii) Group V.

The infant was only seen to allogroom the adult female. The adult male groomed the adult female 3 times as much as the adult female groomed the adult male. The adult female and the infant groomed each other equally.

3.1.1.3. Role changing in allogrooming interactions.

The numbers of times 2 allogrooming individuals switched roles, i.e. the groomer becoming the groomee and vice versa ('reversals'), was not simply a function of the numbers of times those 2 individuals allogroomed each other. Altogether in Group P 'reversals' were seen on 92 occasions. 14 of these (15%) occurred between the adult male and O2 a relationship accounting for only 9% of the allogrooming bouts.

Those individuals which allogroomed the most overall, however, were also those most involved in reversals ($r^S = 1$; $n = 5$, $p < 0.01$). Those individuals most involved in reversals were not those who were the most allogroomed ($r^S = 0.47$; $n = 5$).

Reversals of grooming direction were observed in Group V on 19 occasions. The adult male allogroomed the adult female 35 times with no reciprocal allogrooming from the adult female. The adult female never allogroomed the adult male without a reversal occurring.

In both groups reversals occurred up to 5 times within a single continuous bout, but there was no tendency for those individuals starting a bout to be those which terminated it (Table 8.11). I received the impression, however, that a real difference was present and probably hidden by the short 'request' allogrooming that sometimes initiator finishes bout

Number of reversals:	1	2	3	4	5
GROUP P	25	7	5	4	1
GROUP V	11	6	0	1	1
TOTAL	36	13	5	5	2

TABLE 8.11. Frequency of role switching (i.e. number of 'reversals') in allogrooming.

occurred. Analysis of the data could not confirm this impression as no criteria could be resolved as to what constituted a 'request' and what did not. Despite multiple-reversal bouts occurring, the distribution of time spent grooming by each partner was usually very unequal. In a single bout in which A first groomed B and in which, say, 4 reversals subsequently occurred (i.e. ABABAB) it was commonly the case that each of A's allogroom sessions were short and each of B's long.

3.1.1.4. Contexts in which allogrooming occurred.

The function of allogrooming in juvenile, sub-adult and adult *Indri* is unknown. Animals certainly consumed hair and probably skin they combed from others, though this was infrequent and one may hardly suppose a nutritive function. Allogrooming sometimes followed an aggressive interaction between two animals:

".... O3 annoyed with O2 behind him cuffs him with his elbow. O2 whines, and then grunts and kisses*. O3 moves to another tree followed by O2 and these two spend a lot of time allogrooming during the next 20 minutes ...."

Allogrooming sometimes occurred after individuals had been temporarily separated for a short time. Some measure of reassurance may have been communicated both at these times and when the group suffered a considerable disturbance ".... after a confrontation with a neighbouring group the Group V adult male returns to the adult

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*Vocalisations emitted by disturbed animals.

female from the border region and immediately approaches her and allogrooms her for some minutes ...."

The adult male of Group V often approached the adult female after sleeping and allogroomed her briefly before starting to feed in the morning. At one point I interpreted this as a 'request' to feed. The impression was also gained that during the day allogrooming by the Group V adult male of the female was associated with feeding 'approval' or request - especially after the female had finished feeding in a tree and before the male moved to her exact, vacated position.

Individual idiosyncrasies in allogrooming techniques were evident. In particular, the adult female and O1 of Group P engaged in longer, less intense bouts of allogrooming or licking movements of the head and especially, ears, that were never seen in other pairs. The adult animals of Group V nearly always groomed back-to-back rather than facing or half-facing each other.

3.1.2. Play-wrestling.

Only during the longer activity periods of the summer months (Circuits III and IV) did *Indri* play together. This activity took the form of silent contorted wrestling bouts lasting from a few seconds to 15 minutes. Play was often interrupted or preceded by allogrooming sessions and could end in aggressive displacements with animals - sometimes both the displaced animal and the animal which effected the displacement - clearly disturbed.

This did not, however, seem to affect their immediate subsequent motivation for repeated play-wrestling.

Play was most often performed by young animals. The activity itself consisted of usually two (and rarely three) animals grasping each other with one arm, the other arm being used to hang on to a horizontal bough, and pulling, tugging, kicking and pushing the partner with the feet (Plate 5.1). Unless the bout ended in displacement, the activity was silent and could be interrupted if strange sounds came from the forest or the observer.

Play was identical to that observed by Jolly (1966) for Propithecus verreauxi verreauxi, with the exception that she described no play invitation gestures which were common in Indri and instantly recognisable. An animal soliciting play from another approached to within about 7 metres and observed the future play partner whilst hanging by one arm and extending the other towards the chosen individual. This invitation would be either ignored, or, more usually positively responded to by approach, contact and play. By adopting this same posture the observer successfully solicited contact with the sub-adult in Group P.

Over the year, 120 bouts of play-wrestling were observed in Group P and 14 in Group V. Circuits III and IV accounted for 87% of the year's play bouts in Group P and 10 (or 71%) of the 14 bouts in Group V occurred in Circuit III. Play in Group V was momentary and only involved the adult male (always the initiator of play) and the infant (who always terminated it). The following discussion, therefore, concentrates on the relatively frequent play bouts in Group P.

The time spent in play by the whole group over the year was less than 1.2% of the active period.

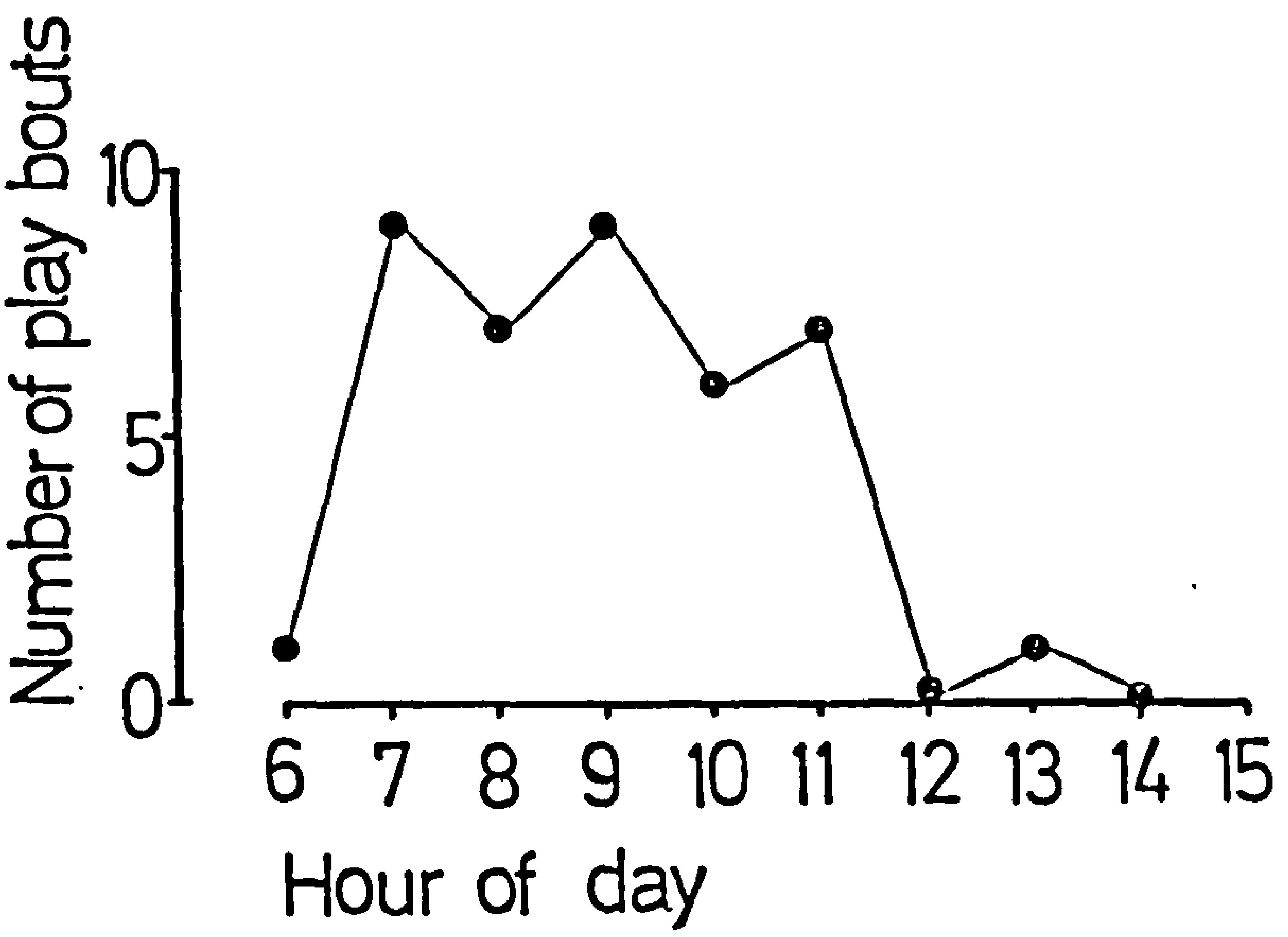
The temporal distribution of play bouts differed between Circuit III and Circuit IV. In Circuit III play was only seen in the morning (Fig. 8.7), comprising 3.2% of the activity period each day. In Circuit IV play bouts were distributed before and after long daily feeding sessions on Cryptocarya olseodaphnifolia fruit, which dominated the ranging behaviour and diet of the group at that time (see Chapter 6 and Fig. 8.7).

Play was seen on every day during Circuits III and IV, varying in daily frequency from 1-8 bouts, although on one exceptional day in Circuit IV 15 bouts were observed.

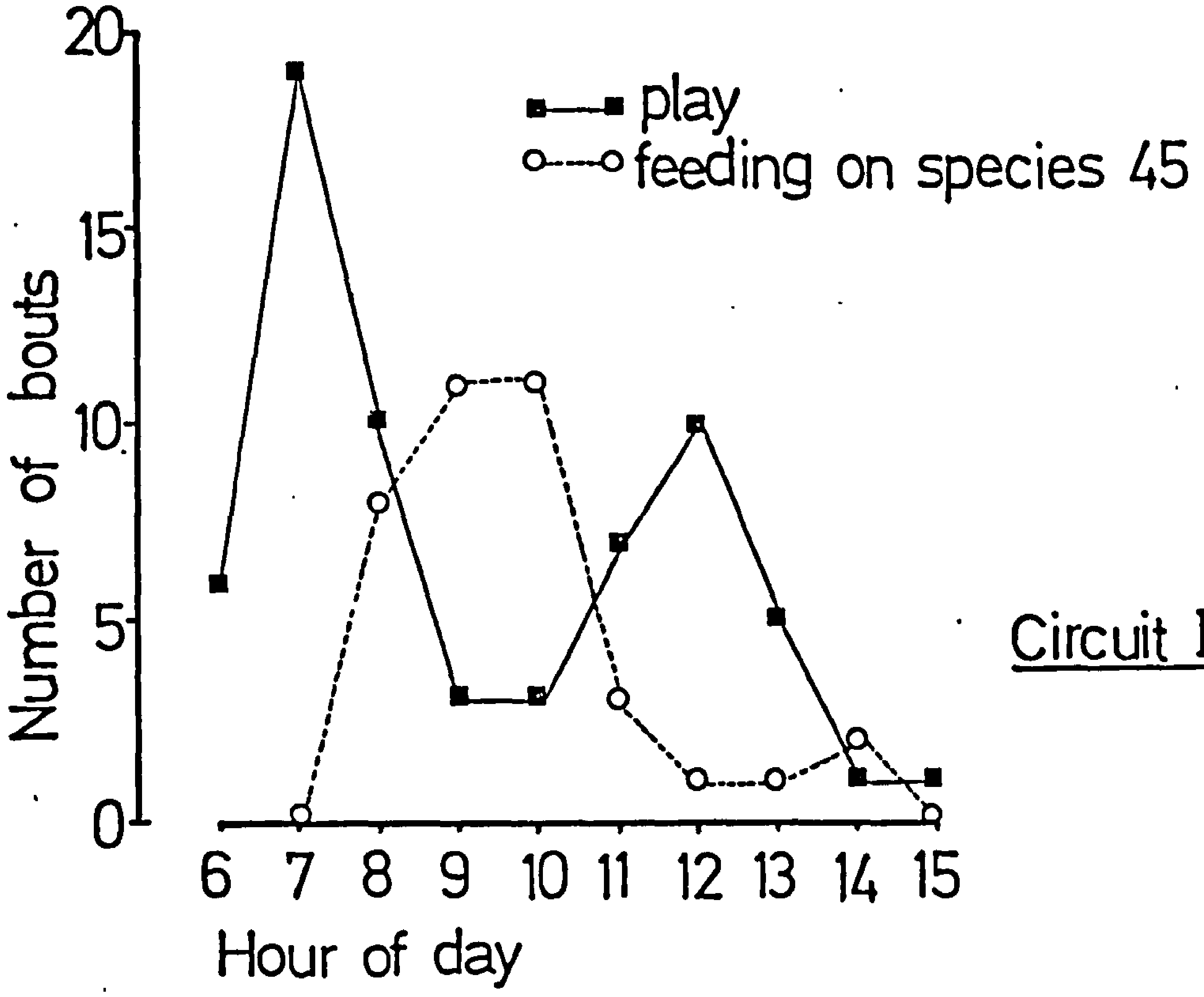
On one occasion play was observed on the ground, but normally it was restricted to sub-canopy or 'canopy bottom' positions between 20 and 50 feet high, where large branches capable of supporting the animals in this (sometimes structurally demanding) activity were present.

15 bouts of play were timed, ranging from 1-15 minutes ($\overline{X}$ = 4.8 mins), but these figures were probably biased towards longer playing sessions as these were the easiest to time.

Figure 8.7 Hourly distribution of play in Group P during Circuit III and Circuit IV. The hourly distribution of feeding bouts on Species 45 is also shown for Circuit IV.



Circuit III



Circuit IV

3.1.2.1. Individual variation in play-wrestling.

Individuals' tendencies to participate in and initiate play bouts varied widely within Group P (Table 8.12). Altogether, the amount of time spent in play by each individual reflected the frequency with which those individuals engaged in a play bout (Table 8.13), suggesting that mean bout length did not greatly differ between individuals.

The adult female was rarely seen to play and never played with the adult male or O3 individuals. The adult male played mostly with O2 and O1 whilst O3 played only with O2. O2 played with every group member.

Between them, the two youngest offspring played together or with others in 71% of all play bouts. They played with each other in 21% of all play bouts.

3.1.2.2. Play initiation.

Those individuals which played most were also those individuals which initiated most bouts (Table 8.12), but frequencies of the activity were too low to permit individual differences in the proportion of initiated play bouts to be defined. In those relationships in which a lot of playing was observed, namely O2/O1 and O2/O3, each partner initiated play with approximately equal frequencies.

3.1.2.3. Play and allogrooming.

At least 28 bouts of play (27%) involved one or more bouts of allogrooming. In 25 of these bouts the initiator

	Ad♂	03	02	01	Total	%
Ad♀	0	0	3	7	10	4.6
Ad♂		2	10	8	20	9.2
03			31	3	36	16.5
02				45	89	40.8
01					63	28.9

(1) Play bout participation in Group P.

INITIATOR

PARTNER

	Ad♀	Ad♂	03	02	01	Total	%
Ad♀	-	0	0	0	0	0	0
Ad♂	0	-	0	3	2	5	10.2
03	0	1	-	8	2	11	22.4
02	1	2	7	-	10	20	40.8
01	0	0	0	13	-	13	26.5
Total	1	3	7	24	14	49	
%	2.0	6.1	14.3	49.0	28.6		-

(2) Play bout initiation in Group P.

TABLE 8.12. Frequency of play bout participation and initiation in Group P.

	Ad♀	Ad♂	03	02	01	Mean
% time	0.0	1.9	3.9	8.5	5.6	4.0
% participation	4.6	9.2	16.5	40.8	28.9	20.0

TABLE 8.13. Amount of time and % participation spent by each individual in play-wrestling activities (Group P) during Circuits III and IV.

was distinguished. The individual most involved in play, O2, initiated 36% of the allogrooming bouts within these play/allogrooming sessions. Overall, this same individual initiated 49% of play bouts and these proportions did not differ significantly (X^2_{1df}= 0.455; p= 0.5).

No differences were found between individuals in the relative frequencies with which they participated in ordinary play and in play/allogrooming ($X^2_{1df(max)}$= 0.203; $0.5<p<0.7$).

3.1.2.4. Play involving aggression.

These play bouts, which terminated in an aggressive displacement, were not separately recorded, but they frequently occurred between O1 and O2, the latter always being displaced. It was not possible to see exactly when and why play became antagonistic, but some biting was seen and disturbance vocalisations heard before rapid, violent movements and eventual displacement occurred.

3.1.3. Defaecation.

Either immediately or shortly after the animals became active each morning all members of an Indri group would defaecate and urinate simultaneously in sites that would be revisited on subsequent days. Each defaecation session lasted for 10 to 20 minutes, during which time all individuals eliminated together, low in the forest and in a very cohesive group formation where uniquely small inter-individual distances were tolerated. The whole of Group P was often spread at these times about a circle of no more than a 3 metre radius. The context of the activity is clearly non-competitive as individuals were found closer to others than would ever occur in, for example, feeding situations, and there were no agonistic interactions or displacements. The tight group configuration and the well developed synchrony in the activity caused it to be considered a form of social behaviour. Social defaecation developed in the infant at the age of 7-8 months. Both the infant of Group V and the youngest individual in Group P hiccuped for about 5 minutes following every morning elimination.

The function of social defaecation sessions in specific locations is uncertain. The possibility that these acted as an environmental mark in the territory is considered in Chapter 9 . An alternative explanation is that the possibility of parasitic infection or re-infection from faeces was to some extent reduced by localisation of the droppings in certain regions. Finally, when the sleeping dispersion of the group was high animals often re-aggregated each morning (before extensive ranging began) at what turned out to be elimination areas, and these may thus have acted as a temporal marker for subsequent group cohesion throughout the rest of the day.

3.2. Agonistic Interactions.

3.2.1. Introduction.

Nearly all instances of aggressive behaviour between group members in Indri occurred in the context of feeding. On some occasions this was apparently due to competitive intolerance over food itself, in others it probably derived from physical disturbance of one animal's support by another as it leapt, with some momentum, from one tree to another. Most aggressive interactions occurred when many animals were feeding in a single tree. In these cases group dispersion was low and stability of the supporting vegetation poor. Although data were not collected, it was clear that frequent visits to the same tree eventually resulted in a dearth of food, increased animal movement to reach the widely distributed, sparse food items,and, consequently, increased aggression.

In the following discussion the category of agonistic behaviour contains, in addition to aggressive animal displacements (see below), the non-aggressive and seemingly 'voluntary' movements away some individuals performed in response to the presence, approach or change in position of others. Thus the adult male of Group V, by moving away first, would often avoid situations in which he would be in danger of receiving aggression[1]. As this behaviour could often be easily recognised, resulted similarly in an effective 'displacement', and was controlled by a potentially aggressive confrontation with the adult female, it was classified as an agonistic interaction.

Every agonistic interaction involved animal movement and always resulted in one individual's displacement to a lower position, or, occasionally another tree. If the displaced individual did not move a sufficient distance

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[1] It was known that such a danger existed because if the adult male arrived first in a food tree that was regularly visited the adult female would usually aggressively displace him.

the displacing animal might repeat the action. This distance which varied from 1 to about 7 metres, could neither be predicted by the observer, nor could the causes of its variability be recognised.

The activity itself consisted of a positive movement by the aggressor, wrestling, kicking and often biting the opponent which immediately tried to escape by descending the tree. Prolonged fights, or indeed any reciprocal aggression from the displaced individual, were never seen. Disturbance vocalisations (see Appendix 6) were frequently emitted by <u>both</u> animals during these displacements.

In Group V, 28 displacements, all of the adult male and all but 6 by the adult female, included 9 (32%) in which aggressive behaviour was involved. In Group P, 36 (34%) of the 107 displacements recorded involved aggression. No seasonal trend in the frequency of displacements was apparent (Table 8.14), but the numbers of observations of aggression were too small to be sure that seasonal variation was absent.

In Group P individuals varied extensively in the frequencies with which they displaced and were displaced by others (Table 8.15). O2 and O3 infrequently displaced others and were displaced the most. The adult female and O1 were virtually immune from displacements. By far the most commonly observed displacement (21% observations) interaction was of the O3 animal by the adult male. Other common displacements were of the adult male, O2 and O3 by

CIRCUIT:	I	II	III	IV	V	VI	VII	VIII
Group P	9	13	18	10	5	8	22	18
Group V	3	0	3	2	3	2	8	7

TABLE 8.14. Seasonal distribution in the numbers of social displacements.

DISPLACOR

	Ad♀	Ad♂	03	02	01	Total	%
Ad♀	-	0	0	1	1	2	1.9
Ad♂	11	-	0	3	8	22	20.6
03	7	22	-	0	12	41	38.3
02	7	6	12	-	14	39	36.4
01	1	0	2	0	-	3	2.8
Total	26	28	14	4	35	107	
%	24.3	27.2	13.1	3.7	32.7		

TABLE 8.15. Participation and direction of displacements (Group P).

O1; O2 by O3; and O3, O2, and the adult male by the adult female. O2 never displaced O3 or O1.

The ratio between the number of observations in which each animal displaced others and was displaced by others (Table 8.16), isolated the adult female and O1 from the rest of the group. Both these individuals displaced others over 10 times more frequently than they were displaced themselves.

Although neither the adult female nor O1 were ever aggressively displaced, 46% of the cases where O3 was displaced and 28% of the cases where O2 was displaced, involved aggression. Conversely, the adult male was aggressive in 68% of the occasions that he displaced others. O2 was never seen to displace others aggressively. On 16 of the 22 occasions that the adult male displaced the O3 animal, aggression was used and these instances accounted for 44% of all aggressive displacements.

Displacements of one animal by another appeared to serve three possible interrelated functions:

(i) directly prevent group members from competing for foods or supports, etc.

(ii) establish a relationship for potential use in (i) above.

(iii) form an integral part of a social system in which food is located by some animals for others.

(i) The most important consequence of the majority of displacements was the resultant inactivity of the displaced individual, which often rested low in the forest in a position far from food. Not only was this individual

		Ad♀	Ad♂	O3	O2	O1
n_1 (displacor)	:	26	28	14	4	35
n_2 (displaced)	:	2	22	41	39	3
$\frac{n_1}{n_2}$	:	13.0	1.3	0.3	0.1	11.7
Aggressive displacements by	:	8	19	4	0	4
Aggressive displacement received	:	0	5	19	11	0

TABLE 8.16. Direction and inclusion of aggression in Group P displacements.

removed from direct competition for a specific food source, but in many instances he was also 'prevented' from feeding at all.

(ii) The instances where animals moved little or allogroomed following a displacement were suggestive of a different function. It is considered possible that relative status in the feeding hierarchy was maintained through interaction of this kind.

(iii) The frequency with which the adult female and juvenile of Group V approached the feeding adult male (especially towards the end of the study when new regions were being visited) subsequently displacing him and feeding, gave the impression that he was locating widely dispersed foods for them. On some occasions, this occurred with such regularity that the adult female was essentially following the adult male and displacing him soon after he started to feed.

3.2.2. Sexual and Reproductive Behaviour.

No sexual activity was observed in Group V, whose female had given birth the previous year. In Group P only attempted copulations were seen. The youngest individual in this group was at this time about 20 months of age.

Sexual behaviour observed in this group consisted of orientation by the adult male towards the adult female and occasional mounting attempts - all of which were easily rejected by the female by turning, shrugging off the male or cuffing him. No other individuals exhibited any sexual behaviour.

The observed sequences of sexual behaviour occurred mostly between 10th January and 26th February. The male followed the female, sometimes for most of the day, mounting intermittently. Intromission was probably not achieved and the adult female did not give birth that year. Attempted copulations were observed in Group P on the following dates:

10/1, 18/2, 19/2, 26/2, 4/4 : 1973.

Group P was observed from 10/1 until 20/1 (Circuit IV) and from 18/2 until 28/2 (Circuit V) in 1973.

When Circuit IV observations on Group P were commenced the adult female was found to be severely wounded in the back (see Section 4). This clearly prevented her from moving far and she was temporarily unable to range with the rest of the group. It is possible that this seriously interfered with sexual activities.

The most striking feature of the observed sexual behaviour was its daily variability. During Circuit V, when most sexual activity was seen, it was present only on 3 of the 10 days' observations and although some activity may have been missed, it was certainly absent on some days. For example, the adult female was followed on 23/2 and 28/2, but no sexual behaviour was recorded on those days. I followed the adult male on 19/2 and 24/2, but only on the former date were attempted copulations seen,when they occurred five times. During this day the adult male and adult female were seen in the same point-sample scan of the group 83% of the time. Overall they were seen only 30.4% of the time in the same scan.

This variable activity was not affected by adverse weather conditions, as on 18/2 (a day in which cyclonic rain fell almost continuously) 5 attempted copulations were seen.

Perineal changes in colour have been recorded for *Propithecus verreauxi* during or before the mating season (Richard 1974). The genitalia of female *Indri* are normally impossible to see, being covered in thick fur. Following the brief summer period in which sexual activity took place, the genitalia of the adult female (and, possibly, of the 2-year old juvenile) became obvious by a stained appearance of the surrounding fur between 20/3 and 26/5 1973. No similar change was seen in the Group V adult female, but the adult female of Group 5 at Vohidrazana, with a suckling infant, had very distinct genitalia on 15/3 1973, visible from 50 metres with x7 binoculars.

The gestation period of *Indri* is unknown, but probexceeds that of the smaller *Propithecus verreauxi*, which is about 130 days (Petter-Rousseaux 1962). Petter (1962) puts the mating season of *Propithecus verreauxi* between January and March and Richard (1974a) observed matings over a short period in early March, the female being receptive for 12-36 hours[1]. It is probable that *Indri*, as in the other large-bodied family-living primates: *Hylobates* sp. and *Symphalangus syndactylus*, have interbirth intervals of 2 or 3 years - probably usually the

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[1] This receptivity period was inferred from the duration of vulval flushing in *Propithecus*.

latter. From evidence presented in Chapter 4 and the research of Petter-Rousseaux (1962, 1970) and others it is possible to state with near certainty that *Indri* have a restricted, seasonal mating period in the middle or towards the end of the wet season, producing infants in May (an infant was born to Group IV at Vohidrazana in the middle of May) - as do *Propithecus verreauxi* in the drier, seasonal forests of the west and south. In the rain forests of the east, *Avahi laniger* were observed carrying young infants at the same time and it is possible, therefore, that this characteristic is typical of the Indriidae. Births at the beginning of the dry season may be followed by weaning at times of relatively high food productivity i.e. the start of the next wet season (see Chapter 4).

4. INDIVIDUAL AND GENERAL RELATIONSHIPS

For both Group V and Group P the most obviously affiliative relationship was between the adult female and the youngest offspring. In Group P there were signs, during the course of the study, that these close ties were diminishing as the frequency of nights in which these animals slept apart increased. At all times during the study, O1 was allowed access to all foods when feeding close to any other individual.

The adult females of both groups were dominant in their ability to displace other animals (apart from the youngest infant or juvenile), although this was infrequently expressed as other animals avoided confrontations. They thus entered little into personal challenges, their social status being apparently assured and automatic. Despite this, few other elements of control or leadership were obviously manifested by the Group P adult female. It was clear that she did not provide, for example, a social 'centre' to and from which other group members moved, because the numbers of animals seen when different individuals were followed did not greatly vary (Chapter 2).

The role of the adult female in Group P might have been studied by her removal from the group, but a disturbance of this nature was contrary to the aims of the study. However, a situation occurred in which this 'experimental' situation was naturally simulated. Returning to Group P after one month's absence very early in 1973, I discovered the adult female on 9th January with a large wound on the lower part of her back and with much smaller ears (Plate 8.3). Her back still bled profusely and she had apparently suffered the wound only a few days previously. She was, at first, so changed in appearance that she was not recognised, the reduced fur around the ears indicating that the wound had been caused not by a fall, but in a fight. The appearance of the adult male had also changed (his ears were also smaller) and this suggested either that the whole group had been involved in an aggressive border dispute or that the two adults had fought each other. A native worker who lived nearby described to me how on 2nd January 1973 cries from this group had been heard

PLATE 8.3 The adult female (Group P) seen (a) early in the study, and (b) in January 1973 when she was wounded in the lower part of the back. The wound is visible as a dark groove in the fur directly above the tail stump. Note changed facial appearance.

every 20 minutes between 0800 and 1000, suggesting the former interpretation.

As the adult female was unable to jump properly, she could not remain with the group which ranged each day to feed on Cryptocarya fruit in specific trees on the edge of the territory. A division therefore occurred within the group that suggested clues about the nature of the cohesive forces acting in normal social ranging:

(i) The adult female and 01 never slept together during this period, but returned to a normal gregarious sleeping pattern after the wound had healed.

(ii) The semantics of certain vocalisations became apparent. It was known that Indri calls ('song', see Chapter 9) - normally emitted in relaxed morning sessions in response to other groups' calls-would also occur following thunder and disturbances from aeroplanes and other animals. Early each afternoon the adult female gave a short call of identical structure from the centre of the home range where she remained each day. The observer, who followed the rest of the group, was able to record the response of the animals. The adult male immediately behaved with great anxiety, calling in reply and moving off rapidly towards her. Sometimes he would not at first travel very far, but would continue his movement towards the female when she called again, often accompanied or followed by the rest of the group. After establishing contact with the adult female, the group, depending on the time of day, would feed locally and sleep together. The next day an early progression to the same feeding trees occurred and the pattern would be repeated. Whether the group would have assembled together in the absence of calls was impossible to ascertain. Without the female the adult male appeared to regularly lead activity and group progressions.

The wound stopped bleeding on 11/1 and the next day the adult female could move slowly in small, low jumps. On 13/1 she moved over 5 quadrats (approx. 220 metres), only one less than the rest of the group. On 18/1 the wound was seen to be bleeding again and though she tried, she did not succeed in keeping up with the rest of the group.

On the first day of the next period of observations (9/2), the adult female's locomotion had nearly returned to normal. She was ranging normally with the group and fur was regrowing around the wound.

These observations showed that ranging by the group was not solely dependent on the adult female and if she did normally control feeding site movements, another animal could satisfactorily compensate in her absence. It also suggested that as few other aspects of social organisation obviously changed, her absence from the feeding group did not lead to gross alterations in group configuration, dispersion, or social activity.

In contrast to the way in which competitive aspects of intra-group relations were 'protected' from the adult female and 01 in Group P, other group members were continuously involved. Large amounts of directionally biased allogrooming, displacements from feeding positions and several measures of social affiliation were widely variable in these individuals. Where food sources were small it was generally O3 who, if present, would be the least likely to be seen feeding. O3 appeared to avoid socially hazardous situations whereas, in contrast, O2 was often aggressively displaced - especially by the adult male - as a result of exhibiting a much greater degree of social confidence by being involved more than any other animal in social activities of all kinds. The paradoxical social position of this individual (O2) which became alternately involved in extremes both of affiliative and aggressive behaviour, was possibly associated with his intermediary age and size. Only for O2 could an extremely aggressive displacement by the adult female one minute be followed at once by stealing fruit five times from the adult male's hand.

The nature of social competition in feeding situations was possibly influenced and its importance mitigated by, individual 'intelligence'. It may be possible for individuals in one tree to know that a competitive situation exists if they observe (i) associates to be feeding, and (ii) associates to be near. When animals are not supported by the same structure, so that their movements are not directly perceived, competition for food may be less evident. Was this the case, for example, when O1 and O2, supported in VCL positions by different trees, were pulling opposite sides of the same sapling towards each other? Was it that these animals were socially 'compatible' in this situation where every effort to feed by one individual obstructed similar efforts by the other, or was it that a socially competitive situation was not understood to exist? The ability to identify such competition, a problem-solving ability, may be positively detrimental to group existence in *Indri* by increasing aggression and reducing inter-individual tolerance.

Spatial elements of the relationship between the adults of Group V ('role') have been described in Chapter 5 . The present chapter has extended the measurement of 'role' to include relationships between adult IIDs and their relative activity. Social signals mediating the control by the adult female of feeding by the adult male appeared to be (i) the female's movement away from a feeding tree (although this did not always result in feeding by the adult male), and (ii) an allogrooming bout. The adult male, on the other hand, stopped feeding either 'voluntarily' or when the adult female began to feed, or (ii) after being displaced.

Elements of 'role' were recognised in Group P, on displacement of one individual by the adult female, and in at least two other *Indri* groups whose composition was known. This suggested that 'role' was not peculiar to groups containing only two adults (+ infant) or to groups containing an infant. 'Role' was highly variable both between and during Circuits and may have altered according to fluctuations in some environmental parameter.

5. SUMMARY: Social Activities.

(i) *Indri* engage in overt social activities for only a minute proportion of the day.

(ii) Differences between individuals in *allogrooming* behaviour could only be clearly recognised when both frequency and direction of the activity were considered together. For example, the adult male of Group P was involved in an average number of bouts but was twice as often the groomer than the groomed. O2 was most involved in grooming but also groomed more often than he was groomed. O1 was groomed on average 2½ times as frequently as she groomed others. In the three possible dyadic relationships between the adult male, adult female and O3, there was little or no allogrooming.

In Group V the adult male groomed the adult female three times as much as she groomed him. The infant never groomed the adult male. Although allogrooming is concentrated upon those parts of the body which can not be self-groomed the social function of grooming is not understood. It never accompanied (although it sometimes followed) aggressive behaviour.

(iii) During the long summer days *Indri*, especially the younger animals, played together several times a day. In Group P 70% of the bouts involved one of the two youngest individuals. Play/wrestling included both aggressive and affiliative behaviour.

(iv) Dominance in Indri was mostly represented by the lack rather than frequency of aggressive confrontations, which were generally confined to feeding contexts. By moving away, some individuals appeared to avoid aggression from others. In Group P, the adult female and O1 were least involved in displacements and were virtually never displaced themselves. The adult male displaced and was displaced equally, whilst both O3 and O2 were themselves displaced much more than they displaced others. Only O3 and O2 were consistently displaced by aggressive interactions. The most common displacement was of O3 by the adult male, and this was always aggressive.

In Group V all displacements were of the adult male, mostly by the adult female.

(v) No complete sequences of sexual behaviour were observed during the study period. Sexual attraction and competition probably play little part in the disruption or maintenance of Indri groups' cohesion and mutual tolerance.

(vi) The role of the adult female in Group P was observed when an injury prevented her from moving far. The rest of the group ranged normally, engaging in unexceptional social activities and returning to the female towards the end of each day. The juvenile O1 appeared to be more independent at this time and slept alone. This change proved to be temporary when the adult female was again able to move normally, after a few weeks.

6. DISCUSSION

6.1. Indri Social Behaviour.

Evidence has been presented in the preceding sections (and in Chapter 5) that the social behaviours found in *Indri* are composed of two main types:

(i) the maintenance of spatial relationships between pairs of individuals, despite the group's cohesive movement about the environment, that are influenced by or themselves influence individuals' activities.

(ii) a low incidence of direct forms of social interaction, often involving physical contact, that occur with different frequencies between different pairs of animals.

It is the purpose of this section to attempt to relate these two forms of social communication to an integrated description of *Indri* social structure.

Some authors have been able to correlate different forms of social interaction between primate group members into unitary concepts of 'dominance' which have a heuristic value in predicting the outcome of wide variety of interactions (Rowell 1966). Others, however, have located a great variability within relationships (Gartlan 1968). The lack of aggression in a relationship between two animals is not necessarily associated, in primate groups, with a high frequency of 'friendly' activities such as allogrooming (Sparks 1967) or play behaviour. The reasons for this are likely to lie in the approaches primatologists choose or are forced to adopt:

(i) In general, antagonism between primates can be clearly recognised and recorded, but tolerated contact interactions, such as allogrooming or play, are claimed to be 'affilitative' primarily because they are not accompanied by aggression.

(ii) The relationship between two individuals may be as much manifested or maintained by a lack of certain interactions as it is by the presence of others. If this is true, relationships which are dynamic or developing may be characterised by high frequencies of social behaviour whilst those which are stable or conservative may be manifested by physical avoidance or spatial tolerance. For this reason it is impossible to comprehend the social organisation of a primate group without monitoring the activities and positions of all the animals at the same time ('latitudinal sampling'). Even this complete knowledge will lack information concerning the manner in which relationships or the society as a whole shape individuals' behaviour over long periods of time.

Possible functions of the few social activities present in Indri groups are considered in Chapter 10 where evidence from observing the ontogeny of social behaviour is suggestive.

Five measures of relationships are presented in ranked form in Table 8.17 for direct comparison. The measures are ranked according to classical interpretations of tolerance or affiliation, e.g. the closest animals are ranked in the same positions as those engaging in most allogrooming and

	Dyad association	Mean distance	0'-10'	Total most allogrooming	Total least displacements
1	Ad♀ - 01	Ad♀ - 01	Ad♀ - 01	Ad♀ - 01	Ad♀ - 01
2	03 - 02	Ad♀ - 02	02 - 01	Ad♂ - 02	Ad♀ - 03
3	Ad♂ - 02	02 - 01	Ad♂ - 02	Ad♂ - 01	Ad♀ - 02
4	03 - 01	Ad♂ - 01	Ad♂ - 01	03 - 02	Ad♂ - 01
5	02 - 01	Ad♂ - 02	03 - 01	Ad♀ - 02	Ad♂ - 02
6	Ad♀ - Ad♂	03 - 01	03 - 02	02 - 01	Ad♀ - Ad♂
7	Ad♀ - 03	03 - 02	Ad♀ - 02	Ad♂ - 03	03 - 02
8	Ad♂ - 03	Ad♀ - 03	Ad♀ - Ad♂	Ad♀ - Ad♂	03 - 01
9	Ad♀ - 02	Ad♂ - 03	Ad♀ - 03	Ad♀ - 03	02 - 01
10	Ad♂ - 01	Ad♀ - 03	Ad♂ - 03	03 - 01	Ad♂ - 03

TABLE 8.17. Correlates between methods of relationship ranking (Group P).

Rank	Ad ♀	Ad ♂	03	02	01
1-5	9	9	5	13	14
6-10	16	16	20	12	11

TABLE 8.17a Mean ranks of individuals in measures of 'sociability'. The frequency with which each member of Group P ranked 1-5,and 6-10 in Table 8.17.

least displacements. A Kendall Coefficient of Concordance tried between judgements of the ranking in each measure was significant (W = 0.377, X^2_{9df}= 16.96; $0.01<p<0.02$). This proved to be entirely due to the consistent top ranking of the relationship between the adult female and the juvenile 01 (Table 8.17)as when this relationship was omitted from the correlations the degree of concordance was not significant (W = 0.148, X^2_{8df}= 5.92; $0.5<p<0.7$).

The number of observations in which two animals were simultaneously seen has been shown (Section 2) not to be specifically correlated in Group P with the mean distance or the frequency of small (0-3 metres) distances by which the individuals were separated. The frequency with which 2 animals were seen in the same scan was not correlated with the frequency of allogrooming (r^s= 0.02). The frequency with which two animals were close together was not correlated with a low frequency of displacements involving those two animals (r^s = 0.43, $p>0.05$), but most allogrooming occurred in those pairs which remained closest together (r^s = 0.636, n= 10; $0.01<p<0.05$).

The fact that type rather than frequency of interaction was a better guide to understanding some forms of relationship in <u>Indri</u> was emphasised by attempts to correlate between relationships different measures of allogrooming and displacements. The correlations tried were (a) total involvement in allogrooming with total involvement in displacements, and, (b) directional[1] involvement

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[1] 'Directional', viz who groomed whom as opposed to who was involved in an allogrooming bout with whom.

in displacements, both of which proved to be non significant ((a) $r^S = 0.267$, $n = 10$; (b) $r^S = 0.129$, $n = 20$). However, when the ratio of the number of times one individual was displaced by another to the number of times it displaced the other was compared with the inverse ratio for allo-grooming viz; $\frac{\text{N Displacor}}{\text{N Displaced}}$ v $\frac{\text{N Groomee}}{\text{N Groomer}}$ - thus ignoring the frequency of interactions - a significant correlation was obtained ($r^S = 0.5595$, $n = 20$; $p < 0.01$). The polarity of the relationships rather than simply the frequency with which the interactions occurred was thus consistent.

Frequencies of social interaction were too low to place great emphasis on individual differences. The gross index of sociability illustrated by mean ranking (Table 8.17a) does suggest differences - especially for O3 (or adult-sized offspring) compared for example, with O1. Measures of spacing in trees also support this conclusion.

Concordance between measures of sociability in Table 8.17 is low, but some relationship (e.g. adult female with O2 or O2 with O1) vary more than others (e.g. adult female with O1 or adult male with O3). The reason for this is not understood but, beyond the mother-infant association, relationships may be more flexible and remain labile until repeated interaction stabilizes them. According to this hypothesis, younger offspring would vary more in their activity towards each other than adults or adults with older offspring.

Measures of activity have somewhere to be brought into this picture of Indri sociality, as it has been demonstrated both in Chapters 5 and 6 and in Section 2 that feeding is of social relevance. In Group V directional attributes of social interactions were consistent and clear: the adult female was always the displacer and the most groomed individual. It was in this group that feeding controls by the adult female or the adult male (Chapter 6) were most obvious. She was, therefore, the dominant animal in all social aspects. Great differences existed in the distances separating adults of Group V between instances when only the adult male was feeding from when only the adult female was feeding. The adult male was tolerated close to the adult female only when he was not feeding. This was not true of the adults in Group P, where other aspects of their relationship were also less overt. The distances between simultaneously feeding adults of the 2 groups were different. Much closer distances in these situations were tolerated by the adult female of Group P than by the adult female of Group V.

Only directional measures of social behaviour may be compared between groups because the difference in group size affected the frequency of behaviour and differences in observer behaviour affected the recorded frequency of social events. These suggest, however, that matriarchy in the two groups differed in degree rather than kind. In both groups contact between adults was infrequent and distance was an important parameter of the relationship.

The influence of the adult female on the adult male's behaviour in each group differed considerably in intensity, but not in direction. Whether this was due to the presence of an infant in Group V, the larger group size in Group P, or the probability that Group V adults had lived together only for a short period in a relatively unfamiliar range, remains to be determined.

6.2. A comparison of Indri and Propithecus social behaviour.

Most aspects of the behaviour of Indri indri and Propithecus verreauxi are similar. They are both large vertical clinger/leapers, diurnal in activity pattern and feed on fruit and foliage in all levels of the forest. Indri, however, live in nuclear family groups - a maximum of 5 animals - whereas groups of Propithecus verreauxi may be found containing up to 10 individuals, often with 2 or more adult males and adult females producing young (Jolly 1966, Richard 1973). Propithecus society, it has been suggested by Petter & Peyrieras (1974) is based on a family social unit, but this has been questioned by Richard (1973, 1974a). In both cases, these authors use group size as the determining characteristic of family groupings and variation in the complement of those groups censused could explain the different interpretations (Pollock in preparation).

There are probably no types of overt social interaction found in Indri groups which are not also performed in similar or identical fashion by Propithecus verreauxi.

The latter do, however, have submissive gestures (teeth baring and tail curling, hunched back posture - Richard 1973) which Indri were never seen to exhibit and some forms of play ('bicycling') which were also absent in Indri (Jolly 1966). Differences were present in the method of allogrooming - P. verreauxi spend 26% of the bouts in simultaneous reciprocal grooming, whereas Indri only groom alternately.

In both species, however, aggression occurred mostly in instances of feeding competition and feeding hierarchies were headed by dominant females. 'Friendly' behaviour, allogrooming and play-wrestling occurred in the same contexts, at the same times and peaked at the same time of the year.

The greater size and changing composition of Propithecus verreauxi groups caused by transfers of adult males between groups during the mating season (Richard 1974), could have considerable consequences on the form and frequency of social interactions. Notwithstanding the differences described above it was not the form of social interaction which varied between species.

Jolly (1966) likened the rarity of social events in Propithecus verreauxi society to that of leaf-eating simians: Colobus and Alouatta. The numbers of social interactions recorded depends on the conditions of observation as well as the behaviour of the animals, and these differed between the forests inhabited by Indri and Propithecus verreauxi. However, most contact social behaviours were obvious and large proportions could be observed and recorded.

Indri and *Propithecus verreauxi* engage in social interactions with a similar frequency (Table 8.18). The higher frequencies of (especially agonistic) interactions in Richard's data for *Propithecus* is most certainly due to her observations during a mating season. Jolly (1966) estimated the total frequency of social events in *P. verreauxi* groups at Berenty to be 0.8 per hour. For *Indri* the total frequency was also 0.8 per hour. These figures may be compared with the relatively 'social' *Lemur catta*, found in large groups of up to 30 individuals, which interacted at a mean of 10.5 events per hour (Jolly 1966). The ratio of the frequency of affiliative to agonistic behaviour differed in the three species: in *P. verreauxi* from 0.2 to 1.0, in *Indri* from 4 to 6 and in *L. catta* 0.4, but this ratio is probably very sensitive to the timing of observations in the year.

As for *Indri*, hierarchies based solely on the frequency of aggressive behaviour and allogrooming in *P. verreauxi*, did not correlate well (Richard 1973). It is considered likely that as no mating season was observed in *Indri*, the full complement and intensity of social behaviour was not observed. Nevertheless, it is unlikely that major changes in frequency of social behaviour would last for long.

The variety and frequency of social activities within groups of *Indri* and *P. verreauxi*, according to the small amount of data available, largely coincide - despite differences in their group size and complement and the

(a) Total

	PLAY	ALLOGROOMING	DISPLACEMENTS	HOURS
GROUP P	109	262	107	526
Group V	7	165	28	359
Total	116	427	135	885
No/hour	0.13	0.48	0.15	

Total = 0.76 events/hour observation.

(b) Interaction per hour

	PLAY	ALLO-GROOMING	AFFIL-IATIVE	AGONISTIC	Totals
GROUP P	0.21	0.50	0.71	0.20	0.91
GROUP V	0.02	0.46	0.48	0.08	0.56

(c) Seasonal variation

		I	II	III	IV	V	VI	VII	VIII
GROUP P	AFFILIATIVE	0.65	0.50	0.99	1.13	0.39	0.78	0.75	0.53
	AGONISTIC	0.25	0.19	0.22	0.11	0.10	0.12	0.35	0.32
	TOTAL	0.90	0.69	1.21	1.24	0.49	0.90	1.10	0.85
GROUP V	AFFILIATIVE	0.28	0.29	0.77	0.38	0.60	0.48	0.56	0.59
	AGONISTIC	0.08	0.00	0.05	0.04	0.06	0.04	0.20	0.19
	TOTAL	0.36	0.29	0.82	0.42	0.66	0.52	0.76	0.78

(1) Indri indri.

TABLE 8.18. Frequency of social activities.

		AGONISTIC	AFFIL-IATIVE	Group size	Total
(a) *P. verreauxi* (Jolly 1966)		?	?	5.0 (mean)	0.16*
Richard(1973)	Gp I	0.29	?	7	?
	II	0.42	0.48	6	0.90
	III	0.25	0.32	5	0.57
	IV	0.44	0.12	5	0.56
(b) *Indri indri* (this study)	P	0.04	0.14	5	0.18
	V	0.03	0.16	3	0.19
(c) *L. catta* (Jolly 1966)					
	1963	?	0.1	20	
	1964	0.31	0.13	24	0.44

(2) *Comparative* (all figures are interactions per animal per hour). *Excludes breeding season.

TABLE 8.18. Frequency of social activities (cont'd).

different environments they inhabit. It is possible, however, that a more fundamental difference exists in the spatial relationships between individuals in the two species or in the control of some individuals' activities by others.

7. SUMMARY

1. Differences existed within groups in the number of times individuals were seen at the same time as others. It was found that the tendency for 2 animals to be seen together when no other animals were also seen did not necessarily reflect their overall measure of association when other animals were present.
2. Although in general the number of times individuals were seen together was negatively correlated with the mean distance separating individuals, this was not always the case. Seasonal variation in the distance and the number of records of distance between the adults of Group V was evident.
3. The distances between adults of each group were different and depended on individuals' simultaneous activities.
4. Differences in the number of bouts of allogrooming given and received did not alone differentiate relationships within Group P. The ratio of donor to recipient in grooming interactions plus measures of overall interaction frequency did.

5. Play-wrestling behaviour is restricted to times of the year when the activity period is greatest and is predominantly an activity of the young. Play involved both grooming and aggressive interludes.

6. Defaecation in <u>Indri</u> is a group activity. Early in the day the group aggregates together and, with low inter-individual distances, defaecates in repeatedly visited sites.

7. Agonistic behaviour occurred mostly in feeding situations. Animals sub-ordinate in aggressive interactions tended to avoid such confrontations. Both measures of frequency and direction of aggression were necessary in order to distinguish relationships . Displacements of one animal by another resulted in the displaced individual resting low in the forest. The function of aggression in <u>Indri</u> groups is considered from these results.

8. No complete sequences of sexual behaviour were observed during the present study. Matings probably occur between January and March - at the same time as <u>Propithecus</u> - and single young are born from about May. In the rain forest all the Indriidae reproduce at the same time of the year with births at the beginning of the dry season.

9. In December 1972, the Group P adult female was wounded in the back. Being unable to move with the group the effect of her absence on individuals' behaviour could be examined. She was able to cause the group to return to her every afternoon by means of loud calls but

otherwise feeding and ranging behaviour were not greatly affected. The close spatial relationship she had with the juvenile was temporarily suspended, only to return when the wound had healed.

10. Overt social interactions are not the only form of social communication in primate groups. Indri studies have shown that the distance separating individuals and their relative positions in trees, influenced their behaviour. Different measures of social affinity between 2 animals did not correlate in this study. Relationships were shown to require analysis in terms of both direction and frequency of social interaction.

11. The frequency with which Indri and Propithecus verreauxi engage in social interactions are similar, despite differences in group size, complement and environment. Most types of social behaviour are very similar but Propithecus verreauxi exhibit a greater variety of social displays.

CHAPTER 9

Inter-group Relations

1. INTRODUCTION

Those aspects of Indri behaviour which are considered to transmit information between groups and other groups or between individuals in different groups are included in this Chapter. These behaviours, which form the social structure of an Indri population, include scent-marking activities, loud calls between groups and confrontations between neighbouring groups at territorial borders.

On first entering a forest inhabited by Indri, the observer is confronted with the impressively loud vocal displays that are emitted during the morning and early afternoon. Over a period of a year each group may call about 500 times and in a study area such as Vohidrazana where at least 40 groups could be regularly heard, the extent of this channel of communication was obvious, conferring on the observer an impression of a 'structure' to the population (see Chapter 11).

In the present chapter an attempt is made at a functional approach to discussions of inter-group (intra-population) communication in Indri. The aims of such an approach are no less than to discover the possible communicative content of olfactory 'marks' and vocalisations. In this study such an approach was limited by 2 factors.

(1) studying the inter-dependence of behaviour amongst groups of animals requires 2 observers to simultaneously follow different groups and to be capable of communicating (by transceiver for example) over long distances.

(2) examination of the communication content of signals necessitates their observation under the total variety of contexts in which they are emitted. Thus as it is probable that communication between groups is of relevance to reproductive behaviour, studies should be made throughout the pre-mating and mating seasons as well as at other times.

For *Indri*, the practical requirements for overcoming these limitations were beyond the scope of this study. Nevertheless, examination of variation in incidence, context, structure and intensity of inter-group communication in *Indri* suggests not only roles of certain signals but focuses on those areas of further research which should prove to be productive.

2. SCENT-MARKING BEHAVIOUR

Indri rub the sides of the mouth and the anogenital region on trunks and branches. This activity is termed 'scent-marking' (see below).

2.1 Cheek-marking

An adult, usually the male, cheek-marks by alternately rubbing each side of the lip and mouth on branches and trunks of between 10 and 25 cms. in diameter, for 2 to 10 seconds. After a short pause this action may be repeated in the same spot. Occasionally the lip is partially everted during this behaviour and it is conceivable that saliva is deposited at these times. No form of glandular tissue, secretion or stain could be seen in the region of the rubbed area.

2.2 Ano-genital marking

Adults were occasionally seen, in the VCL position, to squeeze the vertical trunk and rub the lower part of the body in sideways (males) or vertical (females) movements a few times. The behaviour was often momentary and sometimes only a slight movement occurred. In males this action was sometimes accompanied by the deposition of small amounts of urine, and on one occasion, faeces.

On two occasions observations were made of 'auto-endorsing' (Richard 1974a),where a cheek-marked spot following a small shift in body position was re-marked ano-genitally. In both instances these were performed by the same adult male. The incidence of both cheek-marking and genital-marking[1] by one animal without a change in body position (i.e. marking in two ways the same part of a tree but not exactly the same spot)

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[1] Usually it was impossible to see if the genital or anal region was being applied to the substrate. On some instances the tip of the penis (or scrotal region) or the vulval area was clearly seen to be rubbed, whereas the perianal region was never seen to be used in this fashion. As genital contact with the trunk was identified and anal contact was not identified, the behaviour is best described as 'genital marking' at present.

was seen 6 times in Group P (5 by the adult female and 1 by the adult male) and 3 times in Group V (all by the adult male).

Both forms of scent-marking action varied in intensity from casual contact with the branch or trunk to repeated hard rubbing movements. No external influence on the intensity of the behaviour could be identified. Indri do not mark one another's bodies or obviously display to each other by using marking behaviours. Potential communication through visual aspects of the behaviour cannot be ruled out but the actions commonly occurred when other individuals in the group were out of sight and were, in any case, discrete rather than overt behaviours. Scent-marking never occurred when the animal was in a feeding posture and was usually (and most easily) seen to occur after an individual had made a series of leaps and before another leap sequence began.

2.3 The Frequency of Scent-Marking Behaviours

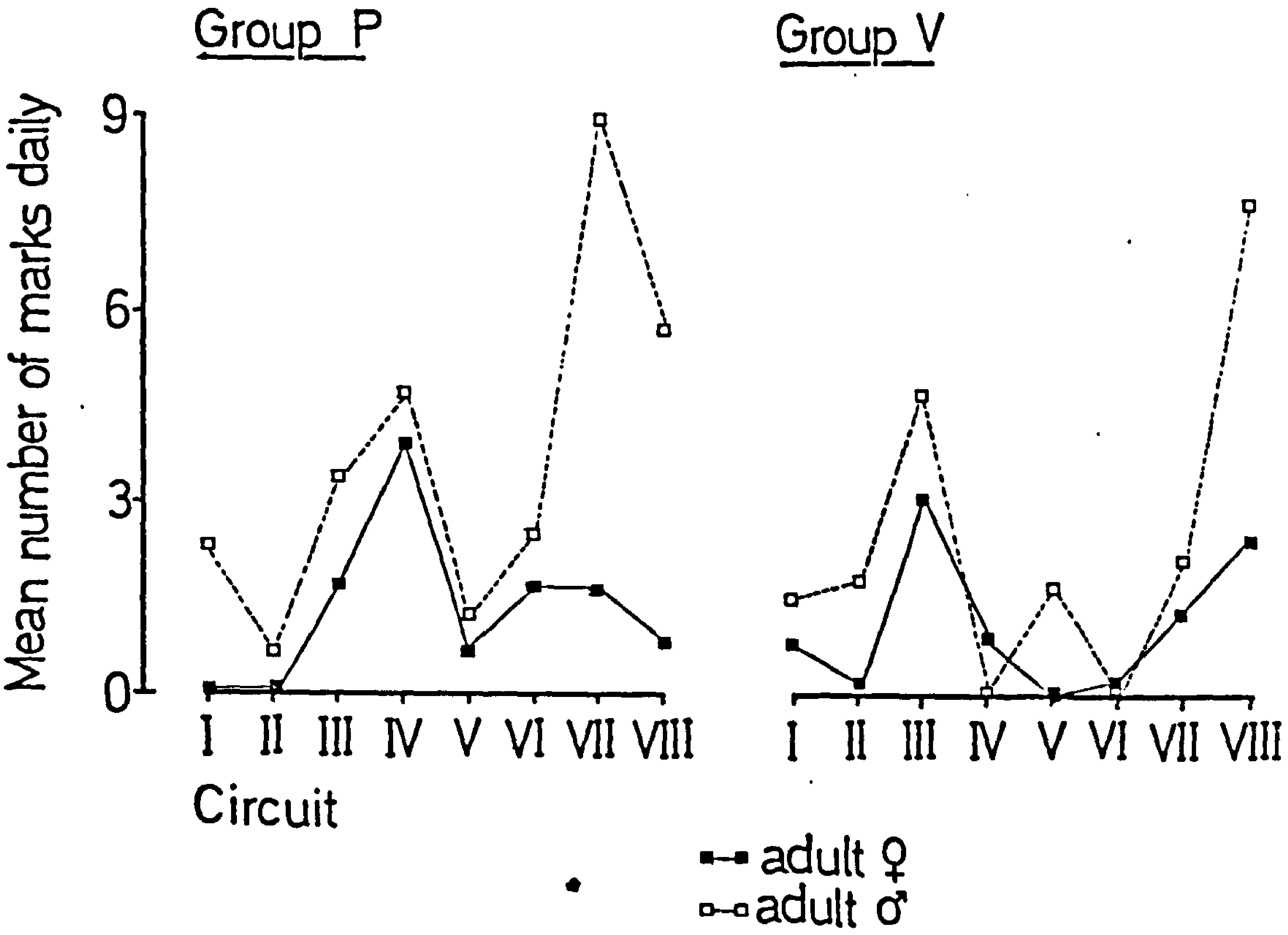
In Group P scent-marking actions were observed on 145 occasions (0.4 per hour) and in Group V on 120 occasions (0.3 per hour). If adjustments are made to account for the differing amounts of time individuals in each group were in view, and assuming the activities of a given individual occurred equally whether that individual was in or out of sight, the adult male of Group P made 70.0% of the scent-marks observed in this group and the adult male of Group V made 71.0% of his group's marks. Corresponding frequencies of the adult females' marking activity were 22% (Group P) and 27% (Group V). In both groups, therefore, virtually all marks were made by the adults and the adult males marked about 3 times as frequently as the adult females. On average the adult males marked 2.9 (Group P) and 2.6 (Group V) times per day, and the adult females 1.1 (Group P) and 1.0 (Group V) times per day.

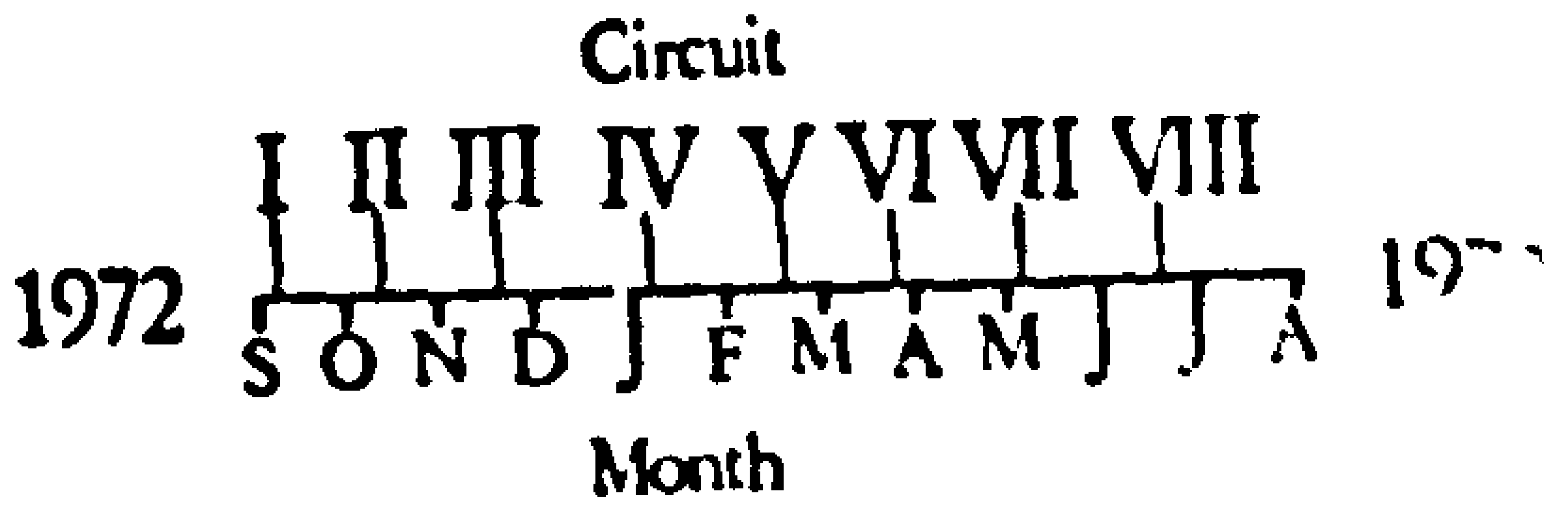
Genital marking was observed on 21 occasions (14% of all marking actions) in Group P - a mean observed frequency of less than 1.3 per day. One third of the genital marks were made by the adult female. 19 bouts of genital marking were observed in Group V (16% of all marking actions) - a mean observed frequency of 0.4 per day. Only 3 genital marks were seen to be made by the adult female of this group.

2.4 Seasonal Variation in Marking Frequency

Interpretations of seasonal variation in scent-marking behaviour are limited by the low general frequency of incidence (Figure 9.1). It is impossible to state, for example, whether the frequency rose significantly or not at the time when some sexual activity was observed in Group P. Both groups appeared to mark more in mid-summer and mid-winter, and except for Circuit VII (Group P) and Circuit VIII (Group V) there was evidence for synchrony in marking frequency between adults within groups.

Figure 9.1 Seasonal variation in the frequency of scent-marking by the two adults in each study group at Analamazoatra.


Group P
Group V
Mean number of marks daily
0
3
6
9
I
II
III
IV
V
VI
VII
VIII
Circuit
adult ♀
adult ♂


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
19
Month

2.5 Daily Variation in Marking Frequency

For both groups it appeared that day-to-day variability in scent-marking frequency was great. As different individuals were followed each day in Group P, this daily variation could not be established with certainty. In Group V, however, the adult male was seen equally from day to day and daily frequencies can be compared (Table 9.1). On 16 (38%) of the days this individual was not seen to mark once, but up to 16 instances of scent-marking were seen daily at other times. Certain days, when scent-marking was observed at much higher frequencies than at other times during the Circuit, were examined for other exceptional features of the animal's behaviour but none could be found.

2.6 The Location of Scent-Marks in Indri Territory

The location of all marks were plotted on maps of the two home ranges (Fig.9.2a-b) to see if *Indri* were marking certain parts more than others. Low frequencies of the behaviour precluded statistical correlations between quadrat use and scent-mark frequencies. It was evident, however, that:

(i) all parts of the home range were scent-marked

(ii) no areas rarely visited were inordinately scent marked.

(iii) territoriallimits, situated on the southern edge of the home range (see Section 3.6), were not preferentially marked by Group P.

CIRC / DAY	I	II	III	V	VI	VII	VIII
V2	3	0	0	0	0	0	12
V3	0	0	0	0	0	2	8
V4	0	2	3	0	0	10	6
V5	0	0	5	1	1	2	5
V6	1	0	5	5	1	1	6
V7	6	7	16	0	0	3	6

TABLE 9.1. Number of scent-marks performed by the adult male of Group V during each day for each Circuit.

GROUP P

(1) By the adult male after being displaced by the adult female
(2) In sleeping position
(3) During a border encounter with Group N
(4) During an inter-specific encounter with Propithecus diadema
(5) When disturbed by a purple Heron
(6) Listening to other groups' calls
(7) After aggressively displacing O3
} Ad♂

(8) Seeing Dr. I. TATTERSALL } Ad♀

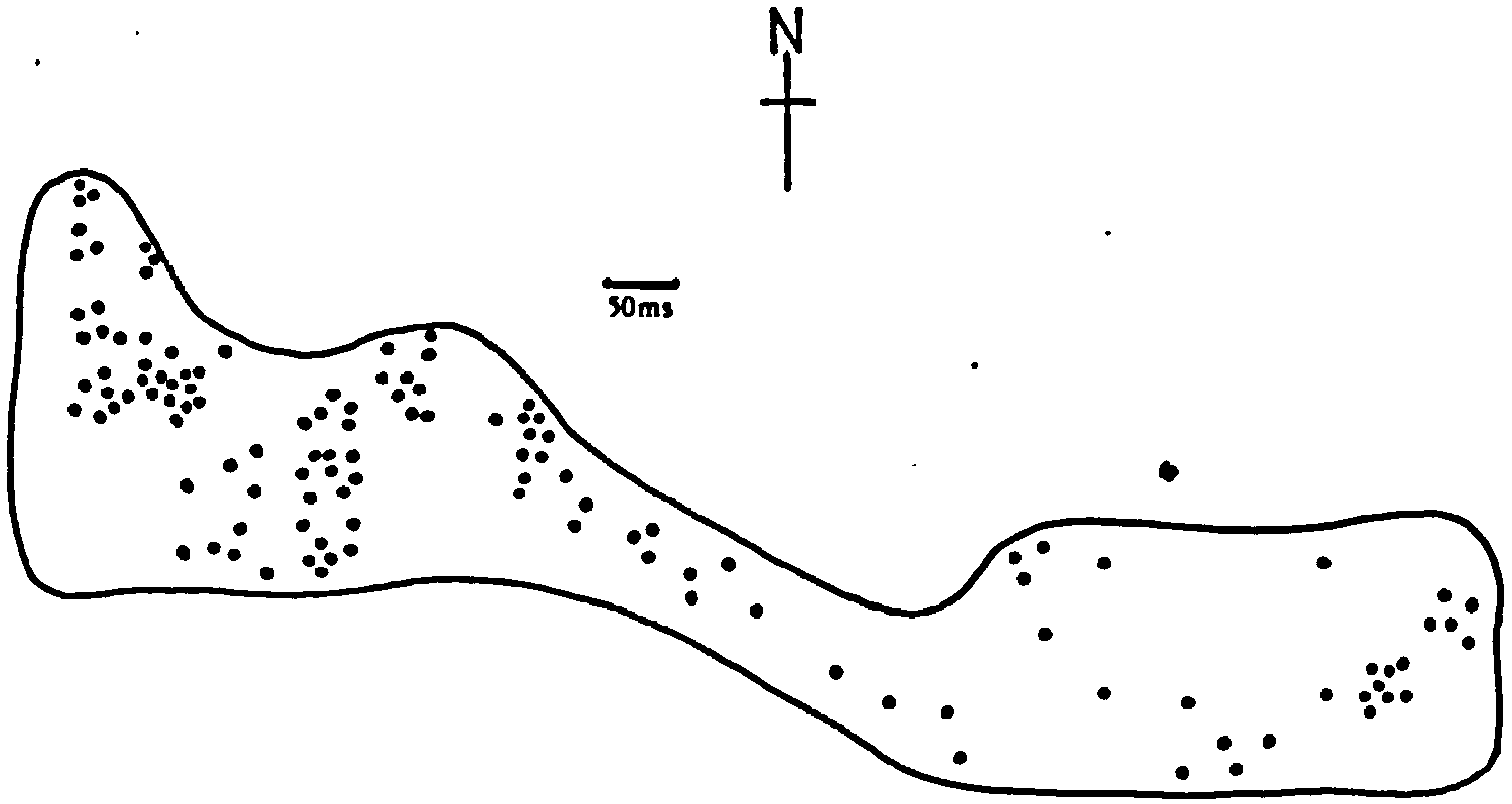
GROUP V

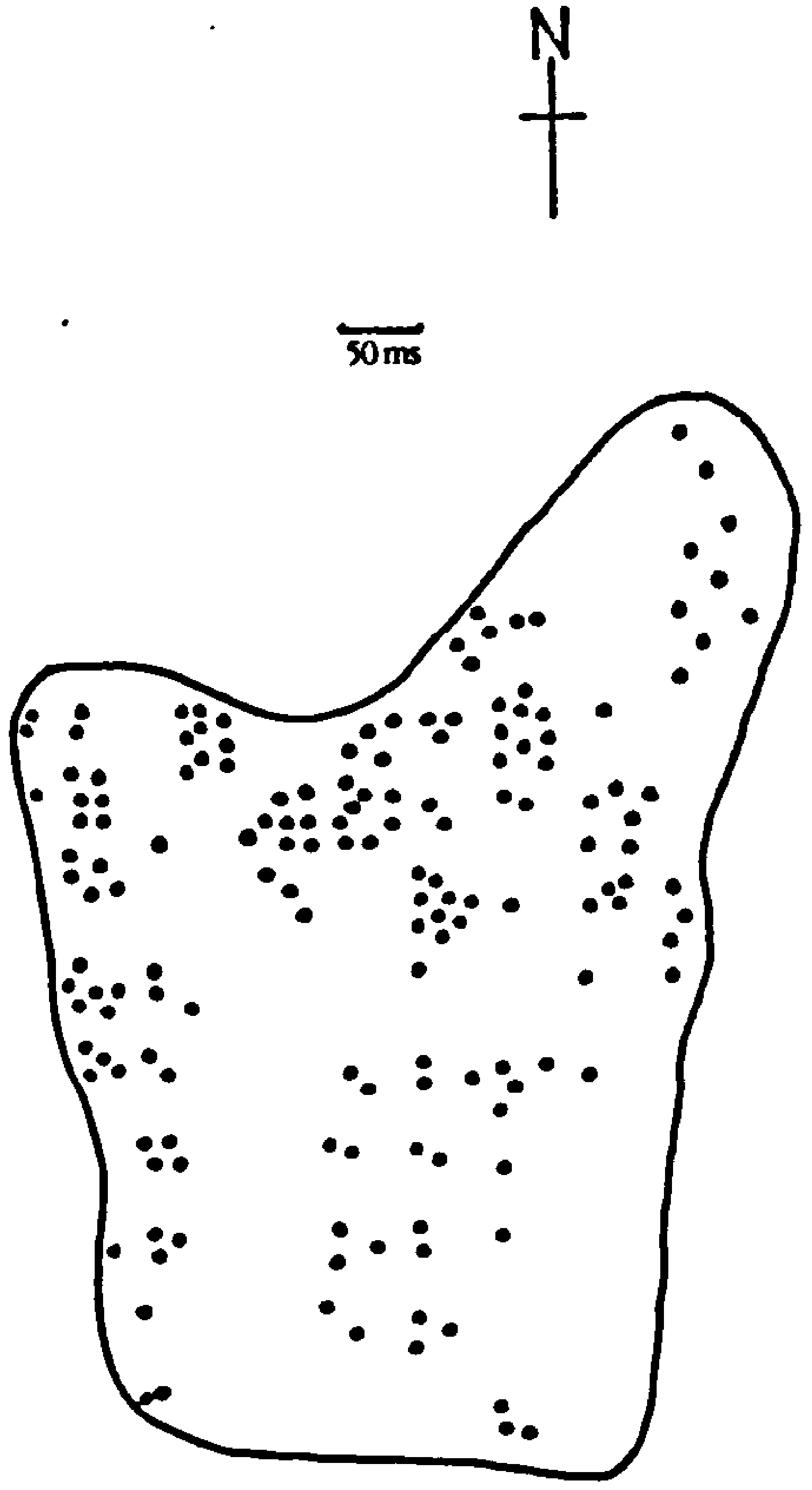
(1) Preceding a loud morning call
(2) Whilst a neighbouring group calls
(3) In sleeping position
(4) When disturbed by a noisy bird
(5) Ranging through an area not previously visited
(6) After allogrooming (the adult female)
} Ad♂

TABLE 9.2. Contexts in which scent-marks were performed.

Figure 9.2a Location of scent-marked spots in the home range for Group P throughout the year.

Figure 9.2b Location of scent-marked spots in the home range for Group V throughout the year.


N
50ms


N
50ms

The only part of the home range where Group V encountered adjacent groups was, however, heavily marked. This area, which was only used for 13.2% of the time, accounted for 31% of the marks. It may be that apparent mark specificity for this region related to the proximity of neighbouring groups, but most marks were deposited during Circuit VIII when only these parts of the home range were used (see Chapter 7). *Indri* of Group V did not specifically mark this area at all times of the year.

2.7 The Function of Scent-Marking

2.7.1 Context of Scent-Marking Behaviour

A hard stare from the observer could often elicit scent (cheek) marking responses from adult males both in the two main study groups and in unhabituated groups encountered during surveys. It can not be ruled out therefore that all scent-marking behaviour was attributable to the presence of an observer. This possibility is considered to be unlikely because:

(i) gross changes in other measures of animal habituation did not correlate with changes in scent-marking frequencies,

(ii) scent-marking occurred on many occasions in specific and repeated spots,

(iii) scent-marking sometimes followed an event very closely, and could be repeated if the same event recurred. These events, or 'contexts' of scent-marking behaviour are listed in Table 9.2.

It should be emphasised that specific events in the environment were not always responded to by scent-marking behaviour. Although no one-to-one relationship existed between any event and scent-marking incidence, the presence of a wide variety of disturbances appeared to increase the probability that the adult male of each group would mark.

The similarly changing frequencies of scent-marking by the adults of each group (Figure 9.1) between Circuits suggests the action of external influences on the regulation of marking behaviour. Observations of marking behaviour as a 'response' to stimuli from the environment support this view. However, in Group V, those days when most marking performed by the adult male was seen were not necessarily those days when the female marked most as well ($r^s = 0.07$, $n = 26$) and unless males and females marked in response to different stimuli, this suggests that internal factors may be important in eliciting marking behaviour.

2.7.2 The Function of Scent-Marking in Mammals

Scent deposition and marking behaviour are widespread in the Mammalia (Ewer 1968, Ralls 1971, Johnson 1973). Evidence is presented in these reviews for multi-factorial explanations of scent-marking, as the contexts in which the behaviour is performed encompass responses to both novelty and familiarity, to territorial maintenance and to situation in unknown regions, to disturbing or foreign stimuli and to group members. Common denominators found across the mammals are (i) sexual dimorphism in deposition frequencies and (ii) seasonal variation (or variation deriving from reproductive parameters) in marking incidence (Johnson 1973).

The most frequently considered functions of scent marking in mammals are:

(i) Territory or home-range delineation
(ii) Territory-definition and occupation
(iii) 'Ownership' of objects, places, other animals
(iv) Advertisement of personal characteristics: reproductive state, age, dominance, sex and perhaps genetic relationship
(v) Population regulation

There are no references to strict boundary scent-marking in free-ranging mammals, although the periphery of cages or enclosures are frequently scent-marked (Lindmann 1955). Aleksiuk (1968) describes territory-edge marking in a wild beaver colony, but a satisfactory proof of territoriality is absent.

There are many instances in which mammals have been found to mark throughout their home-ranges and territories (Mykytowycz and Gambale 1969, Goddard 1967, Strandgaard 1972) and even in neighbouring territories (Myers and Poole 1961, Mykytowycz 1965). In these cases, marking may serve to display occupancy of a territory rather than its geographical limits. Specific individual or group characteristics might also be communicated over a period of time by scent-marking. Scent-gland activity in several species can be experimentally controlled by changing hormone levels (Thiessen and Lindsay 1970, Mykytowycz 1965) and animals in a reproductive condition may scent-mark more (Johnson 1973)

Familiarity with objects and conspecifics is also correlated with scent-marking in some species (Rosenblatt, Turkewitz and Schneirla 1969, Gregory and Pfaff 1971) and may afford a means of individual recognition (Harrington 1971, 1974).

Unless odours emanate from a source with decreasing gradient, directional quantities in olfactory communication by lemurs are lacking. Route finding and orientation may be mediated through successive scent-marks in certain directions or their role in positioning the animal in the home range may be indirect. An animal may be reminded, for example, by olfactory clues that a certain stimulus which previously evoked a scent-mark (e.g. a predator) greeted it on its last passage through a specific area and thereby cause it to avoid that region in the future.

Scent-marking finally, has been considered to form an intimate constituent of courtship (Sikes 1971, Mykytowycz 1965, Ewer 1968), recognition of group membership or 'ownership' (Schultz-Westrum 1965) or to be a measure of animal density (Wynne-Edwards 1962, Alelsiuk 1968). It is very often exhibited by disturbed or aggressive animals and usually accompanied by displays or semi-permanent visual signs of environmental alteration (Jolly 1966, Ewer 1968).

2.7.3. Scent-Marking in Primates

Observations of scent-marking activities and/or the presence of scent glands have been recorded throughout the primate order but notably in the infra-order Lorisiformes and the superfamilies Ceboidea and Lemuroidea. In the Cercopithecoidea, Hill (1953) has described the existence of a 'sternal gland in Mandrillus leucophaeus and observations of cheek rubbing by Cercopithecus aethiops (Gartlan and Brain 1968) have been reported. In the South American monkeys sternal glands are known to exist in Ateles (Hill 1953), Callicebus (Moynihan 1966), Pithecia, Alouatta, Cebus, Cacajao, Saimiri and Lagothrix as well as throughout the Hapalidae (Epple and Lorenz 1967). These glands reach their full differentiation in adults, especially in males, varying in location from the epigastric to gular regions. Within the Hominoidea only the orang-utan is claimed to possess such a structure (Schultz 1941) and this is rudimentory. Homo, Pan and Gorilla have axillary glandular concentrations of specialised sweat glands. Axillary and pubic hair may concentrate apocrine secretions in these areas (Goodhard 1960).

Most lorises and bush-babies engage in 'urinewashing' or urine (and, sometimes, faeces) deposition (Andrew 1964, Doyle 1974), but specialised scent glands are generally absent.

Most if not all, lemur species scent-mark - often in several ways. Urine and faeces may be dropped or smeared by small lemurs with no overt glandular area : *Microcebus murinus* (Petter 1962), *Cheirogaleus medius* (Petter 1962). Urine marking has, in addition, been recorded for *Propithecus verreauxi* (Petter 1962), *Propithecus diadema* (pers. obs.), *Indri indri* (pers. obs.), *Hapalemur griseus* (Petter & Peyrieras 1970a), *Lemur fulvus* (pers. obs.), *Daubentonia madagascariensis* (Petter & Peyrieras 1970b). Anal, anogenital or genital marking has been observed in *Microcebus* (Petter-Rousseaux 1964), *Lemur catta*, *Lemur macaco*, *Lemur fulvus*, (Petter 1962), *Lemur mongoz* (Tattersall & Sussman 1975b), *Lepilemur mustelinus* (Petter 1962), *Propithecus verreauxi* (Jolly 1966), *Propithecus diadema*, *Hapalemur griseus*, *Indri indri* (pers. obs.), and *Daubentonia madagascariensis* (Petter & Peyrieras 1970b).

Specialised gland-like structures which either secrete or store a secretion for dispersion are found in the antibrachial region in *Lemur catta*, *Lemur macaco* and *Hapalemur griseus* (Petter 1962, Jolly 1966) and on the forehead in *Lemur macaco*, *Lemur fulvus* (Petter 1962) and *Lemur mongoz* (Tattersall & Sussman 1975b). Structures of different or homologous origin are also found in *Lemur catta*, *Hapalemur griseus* (axillary region): *Varecia variegata*, *Propithecus verreauxi*, *Propithecus diadema*, *Phaner furcifer* (neck, throat): *Indri indri* (cheek) and *Avahi laniger* (gular). No species possesses more than one paired gland in these regions.

A territorial context has been generally attributed to lemur scent-marking activities by previous authors. Jolly (1966), for example, includes scent-marking in "...the section on inter-troop behaviour, since scent distinguishes a territory, even in the owner's absence and a territorial dispute involves a frenzy of scent-marking, urination and defaecation ...". Where there is information, it seems that scent-marking is most often performed by males, during the reproductive season and in inter-group encounters (Jolly 1966, Richard 1974a). Possible functions of orientation, and sexual stimulation, individual identification and identification of sexes, social groups and taxa are suggested by Harrington (1971), following his specialized study of olfactory communication in wild and captive *Lemur fulvus fulvus*.

Those species of primate which have been seen to scent-mark, inhabit forests of considerable vegetational density. It is not understood how far olfactory signals carry in the wild, but strepsirhine primates may require additional means of communication in environments where visibility is poor. Olfactory communication may be especially important to primates with a small repertoire of vocalisations living in dense, arboreal habitats and retaining for the most part nocturnal patterns of activity.

2.7.4. Scent-Marking in Indri

As no glands are visible in living *Indri* and no traces of glandular tissue can be located on the skins of dead specimens, it is possible that the performance and function of scent-marking is vestigial. Alternatively the activity is primarily a visual display, or a relatively fine control of the behaviour directs a powerful and delicate form of olfactory communication.

Great contrast was evident in the eastern rain forests of Madagascar between the quiet *Propithecus diadema*, whose males had long stained patches of dark fur on the upper chest which they rubbed intensely on tree trunks every few minutes, and the noisy, vocalising *Indri* whose scent-marking behaviour was infrequent and short-lived, with perhaps no olfactory substance even deposited.

The suspected functions of scent-marking and *Indri* 'song' will be examined in Section 4 .

3. INDRI VOCALISATIONS - THEIR STRUCTURE AND FUNCTION

3.1. Introduction

Forests inhabited by *Indri* resound each day with loud modulating calls (song) emitted by whole groups. The members of each group call together either (apparently) spontaneously or in response to other groups' calls, or following disturbances such as strange noises, thunder, the calls of other lemur species or the presence of birds or aeroplanes. The two study groups both called at least once on 69% of the observation days, but as many as 7 calls could be emitted daily. Both groups and the surrounding population called mostly during the morning and in the summer months. In December calls were heard at all times during the night in all study areas.

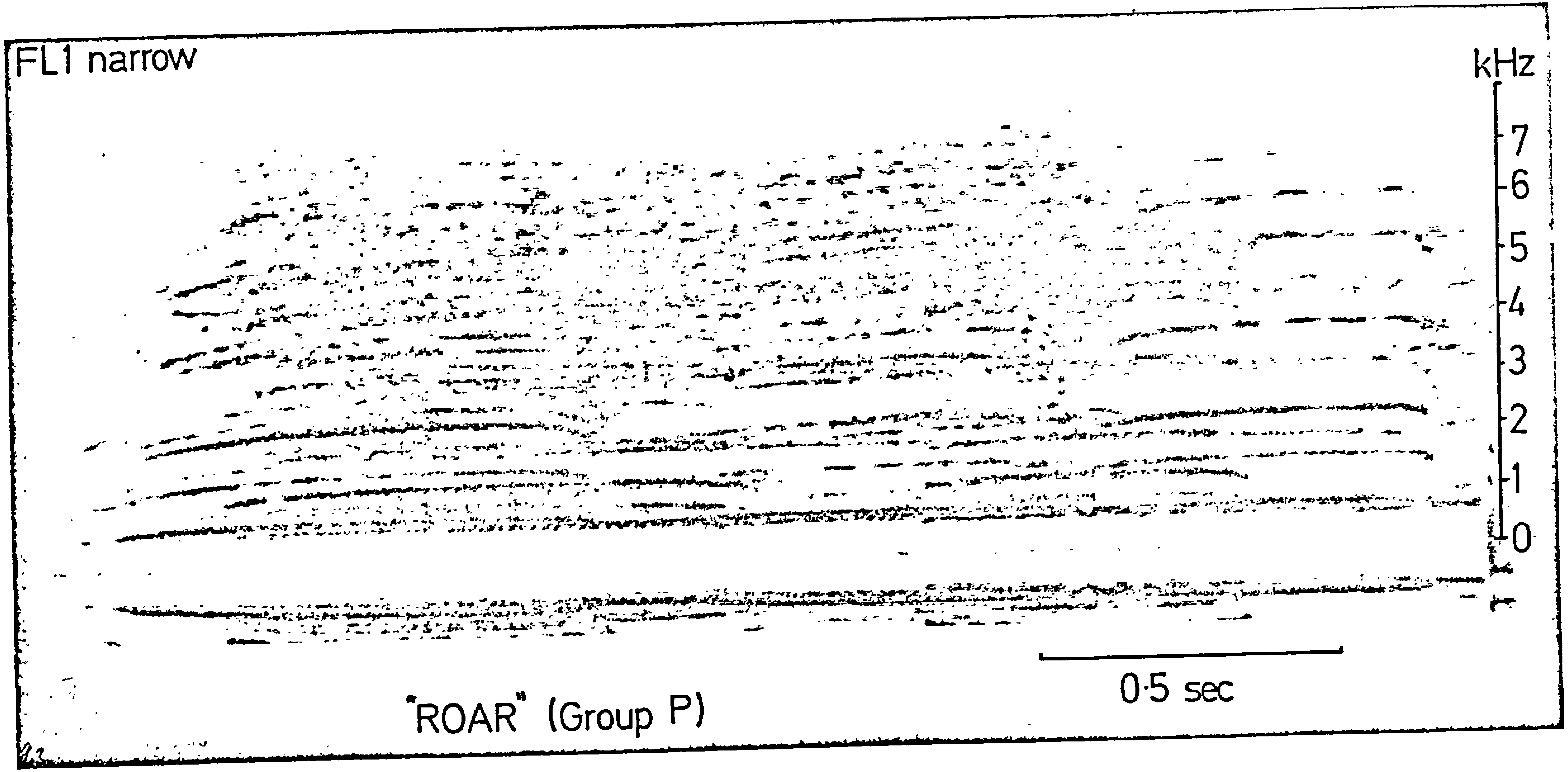
3.2 The Structure of Indri 'Song'

Sound producing or amplifying structures possessed by primates with loud calls are very diverse. The specialised hyoid in howler monkeys and inflatable throat sac in *Symphalangus* provide extreme examples. The vocal sac of *Indri* is probably instrumental in producing gain in the continuously modulating tones, but presumably plays little or no part in pitch changes (Andrew 1963). The mechanism of sound production in *Indri* is not known.

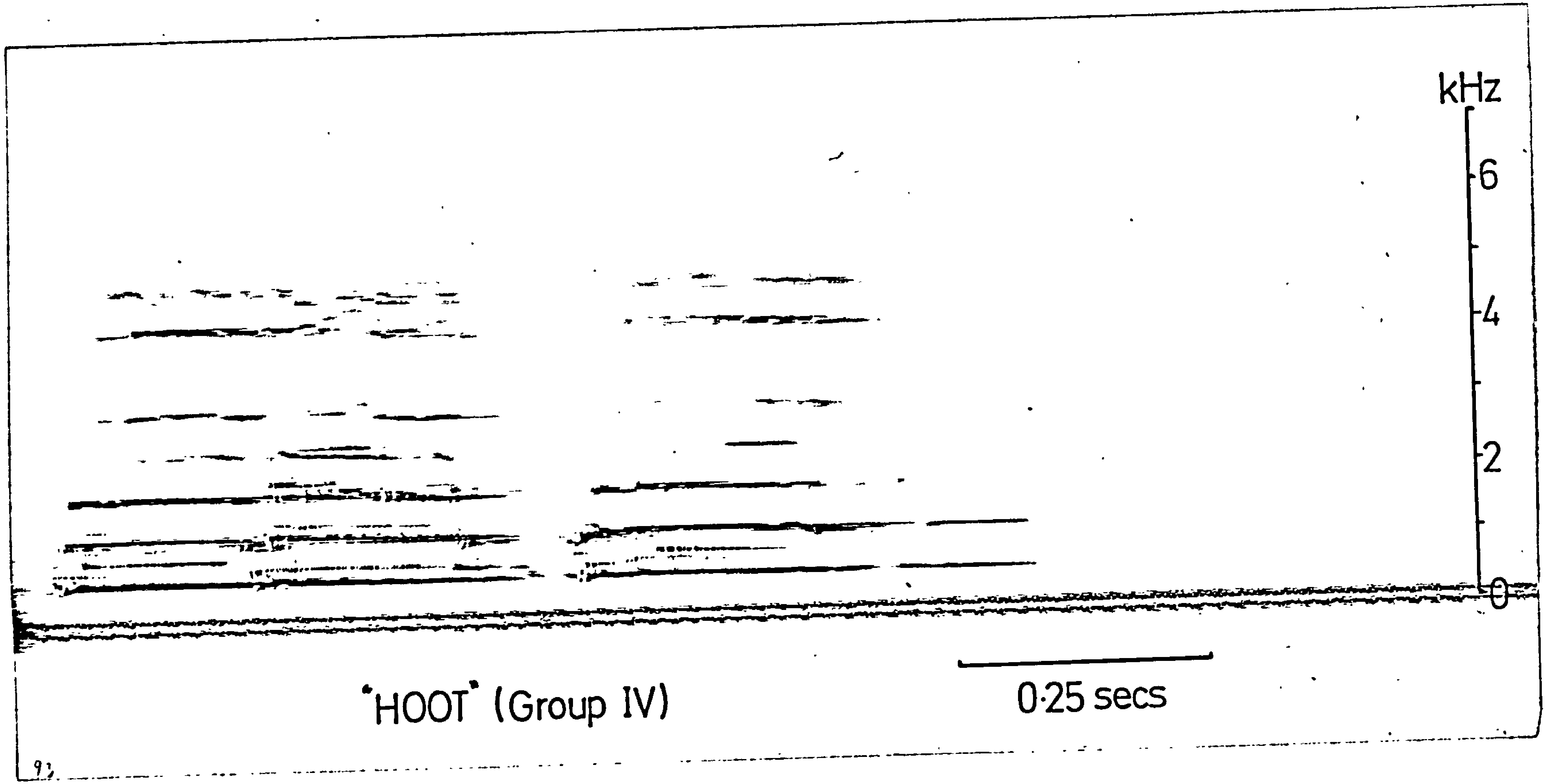
Calls in the field were recorded on a Nagra IVL portable tape-recorder through a Sennheiser MD421N super-cardioid microphone on BASF standard and low noise magnetic tape. Frequency response characteristics of all components were essentially linear in the relevant spread of pitch. Recordings were made of the study groups' calls on one or two days each Circuit, from a position between 20 and 100 feet from the calling animals which were often quite dispersed and rarely faced the microphone. Modulometer scale readings repeatedly confirmed a maximum intensity of between 110 - 120 dB within 5 metres of a single individual. This amplitude was near to the pain threshold of the observer. The call could be heard by the observer between 1000 to 2000 metres from source according to the topographical positions of the calling group and the observer, wind speed and direction, and the amount of intervening vegetation.

Each Indri song is often, but not always, introduced by a communal "roar" ("aboiements" - Petter 1962) which normally lasts between 1 and 5 seconds, and occupies a wide band of frequencies between 500 and 4000 Hz (Figure 9.3). This call is identical to that emitted as an aerial predator alarm call (see Appendix 6), and precedes song in 87% of all calls. A short pause (½ - 2 seconds) separates the end of the roar from the song proper - sequences of short howls which last in total for 40 - 250 seconds. Occasionally, the adult male or O3 would move during the roar but usually animals either remained in their feeding positions or took up a secure position in a more central, lower part of the the tree they already occupied. The howls would be emitted in no particular direction (they never turned to face the origin of the preceding call, for example), but the muzzle always pointed between 30° and 45° above the horizontal (Plate 9.1). According to Petter and Peyrieras (1974) Indri call from the tops of trees at the highest parts of the ridge, a position these authors

<u>Figure 9.3</u> Sonogram of *Indri* "roar". Kay Sonograph (Wide-band).



"ROAR" (Group P)



"HOOT" (Group IV)

PLATE 9.1 *Indri* 'singing'. Two Group P individuals photographed whilst singing. The nearest animal is in mid-howl, the mouth rounded and the muzzle pointing upwards.

suggest to be of optimal sound transmission. During the present study, Indri were not seen to behave in this way and it is by no means certain that calls from such positions would in any case carry the farthest (see Appendix 5). Indri call from where they happen to be at the time (see Section 3.6) and were never seen, no matter how low they were, to climb higher before or during a song.

Indri calls are usually relaxed events, despite the enormous power of the sound. On several occasions feeding continued between howls during the course of the song. Non-participants in a group's song (see below) were seen to groom, play and feed whilst others sang.

Once the song ended, normal feeding and ranging activities were resumed. Behaviour following singing by the group in no way appeared to differ from behaviour before the song.

In Group P the communal roared introduction was sometimes preceded by a short, low pitched howl (Type 1 - see Section 3.4). given by the adult male or more rarely 03. The adult male was also the first to start to roar in 60% of the calls in which the timing of individuals' contributions to the song was recorded. The impression was gained that on at least some occasions the adult male may have induced others to sing.

3.3 Individual Participation in Indri Song

Individuals did not participate equally in a group's call as supposed by Petter and Peyrieras (1974). In both study groups however, the two adult individuals figured prominantly in all songs.

(i) Group P

The adult female normally sang throughout the duration of the call. All individuals roared, but 01 either continued for one or two howls only or remained completely silent. 02 always sang more than 01, but did not participate in every call. When 02 did sing, he always joined in at the beginning and, occasionally, in the middle of the song.

The alternative roles of the adult male and 03 in Group P's calling pattern were of great interest due to their change during the course of the study. Normally the characteristic features of the adult male's singing pattern were his introductory howls at the beginning and the invariable calling in duet with the adult female at the end of the call. Between the end of February 1973 and until observations were discontinued in the following July, 03 replaced the adult male in this terminal duet with the adult female. The adult male and 03 never called at the same time during the song. Singing alone with the adult female ('duetting') occurred therefore intermittently and exclusively by the two oldest males - when one started the other stopped, or after one had stopped the other soon started.

(ii) Group V

All members, including the very young infant (see

Chapter 10) roared but only the adults continued into proper song. The adult male began with characteristic long, low howls (Figure 9.4) of fundamental frequency 800 Hz, each lasting 3 seconds, whilst the adult female produced higher, modulating calls sometimes in strict rhythms . Both animals started and ended the call together.

(iii) Group IV at Vohidrazana

All animals also roared in this group. On the one occasion that individuals' singing order was established without doubt, the adult female sang throughout and ended in duet with the oldest (female) offspring.

Many calls in the population had a structure similar to that of Group P, where the difference between adult male and female was distinct. This observation furthered the belief that Indri groups always contained an adult pair, and suggested that some consistent characteristics of song pattern in all groups in the population could be described:

(i) adult females always sang right through the length of the song.

(ii) young animals participated only (a) in the introductory roar or the very first seconds of the song (infant/juvenile), or (b) during the first half of the song (sub-adult).

(iii) the type of call emitted and the synchrony of participation may differ between individuals of a group.

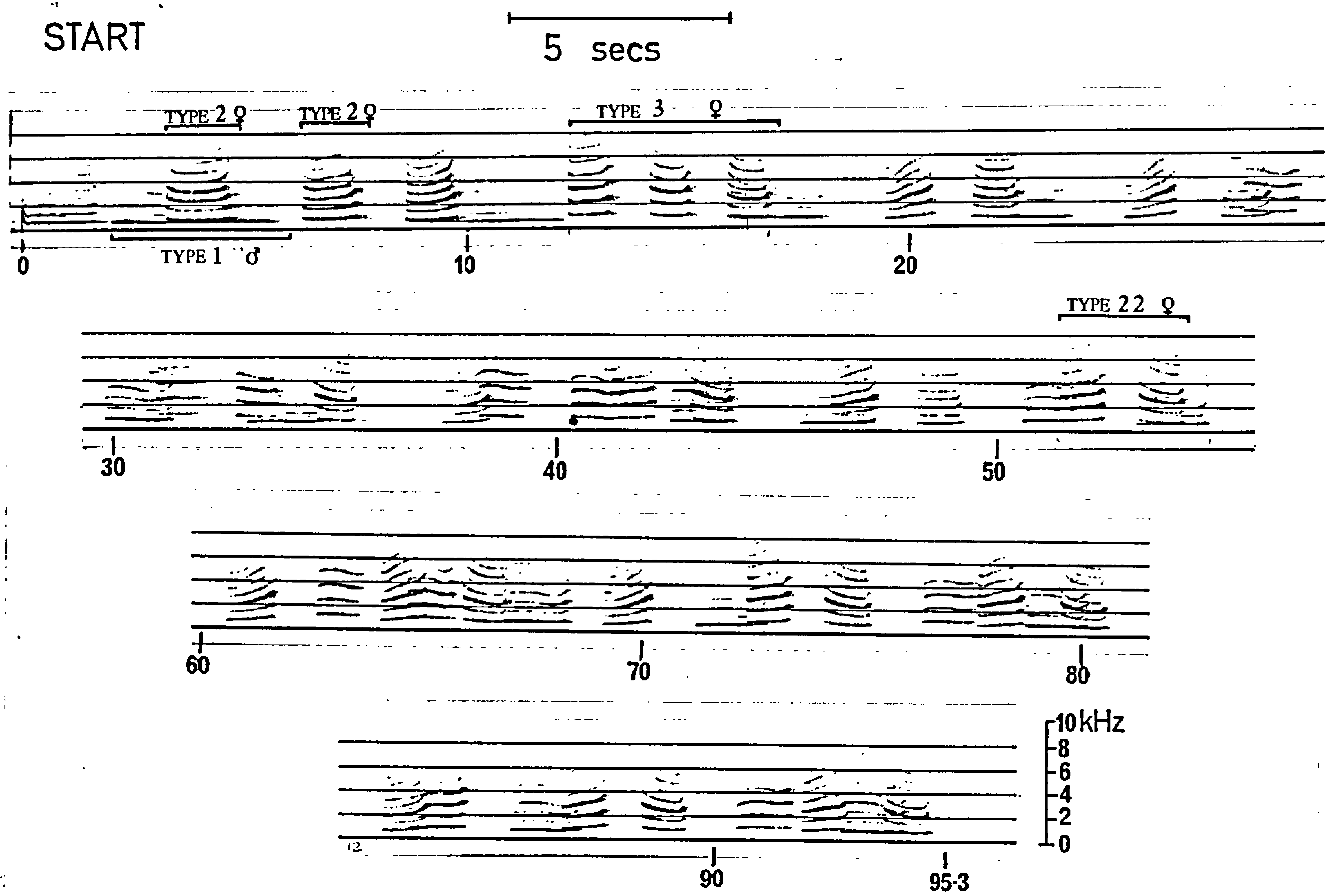
3.4 The Physical Analysis of Indri Song

The structure of Indri calls was examined by means of a Kay Sonograph and a real time sound spectrum analyser (the"Ubiquitous") which was developed and adapted by members of the Rockefeller University in New York. The Kay Sonograph records small lengths of sound from a play-back machine on to a rotating drum and, by applying a succession of different filters, traces a picture of frequency composition (vertical axis) against time (horizontal axis), with approximate measures of amplitude represented in the intensity (or darkness) of the trace. The "Ubiquitous" does effectively the same thing - but by storing, in digital form, very short bursts of sound, it can produce continuous traces and is thus most suitable for long bird or mammal calls which last more than a few seconds.

One complete short song emitted by the 2 adults in Group V is presented pictorially, following analysis by the "Ubiquitous", in Figure 9.4 . The song is seen to consist of a series of wails each lasting from 1 to 4 seconds. The main energy bands of each wail lie in the range 500 to 6000 Hz. Pure tones of the call appear to resonate from at least two chambers with up to 4 harmonics and may modulate by as much as 2000 Hz within each howl. Some howls, however, remain essentially stationary in pitch.

During the course of the study different types of howls within each call were recognised. Some of this variation could be attributed to sexual dimorphism in

Figure 9.4 Continuous sound spectrum analysis of a complete *Indri* song (Group V). 'Ubiquitous' sound spectrum analyser (Rockefeller University, New York).


START
5 secs
TYPE 2 ♀
TYPE 2 ♀
TYPE 3 ♀
TYPE 1 ♂
0
10
20
TYPE 22 ♀
30
40
50
60
70
80
10kHz
8
6
4
2
0
90
95·3

the adults' song:

(i) Type 1 calls

Long, low calls emitted only by adult males, of fundamental frequency 750 Hz with an additional band at 1250 Hz, and subsequent harmonics. Type 1 calls were usually the first calls emitted by the adult males of each group and were most noticeable when only two animals were singing. Each Type 1 call lasted, in the measured examples, for up to twice as long (maximum observed duration 4.2 seconds) as other calls. Little frequency modulation occurred during the course of the Type 1 calls.

(ii) Type 2 calls

Type 2 calls were modulating calls which always ended in a pitch higher (up to 2000 Hz above) than the beginning. Most the energy of the calls resided between 700 Hz and 3000 Hz, but varied extensively in their frequency of attack. Type 2 calls generally lasted from 1.2 to 1.9 seconds and often preceded a similar 'mirror image' call which started at the termination frequency and ended at the initial frequency of its predecessor (Figure 9.4). These paired calls (Type 22) were very typical call sequences, being emitted by all singing individuals.

(iii) Type 3 calls

Type 3 calls consisted of a series of 3 (or occasionally 4) successive howls, each starting lower than the preceding howl in its frequency of attack and normally modulating slightly, twice (Figure 9.4). Each call lasted for the same duration as Type 2 calls, which they very often followed in the song. All animals produced these calls at some time during the song, but they were typically emitted by the adult females earlier than by other individuals. The first call of a Type 3 sequence was the loudest and highest (up to 9000 Hz) containing most of its energy in bands up to 6000 Hz.

In the two songs analysed, the percentage time spent calling by the adult females during the course of the song (omitting the short silent periods between howls) was 28.5% (Group P) and 43.8% (Group V) respectively. Corresponding figures for the adult males were 41.3% (Group P) and 43.3% (Group V). From these percentages it is possible to calculate the expected amount of time in each group's song that the two adults would be calling simultaneously, given that they were calling independently of each other. The expected values, 10.1 seconds (Group P) and 18.1 seconds (Group V) did not greatly differ from the observed time spent in simultaneous calling, 10.8 seconds (Group P) and 14.5 seconds (Group V). It seems, therefore, that each call by each adult during the song proper was not socially organised so as to occur at the same time and thereby achieve a greater production of sound.

In both groups the duration of each male howl exceeded that of the females. In Group P the male called in howls that had a mean duration of 1.8 seconds whilst the mean call duration of the adult female was 1.4 seconds ($t = 4.26$: $p < 0.001$). In Group V the male called for a mean time of 1.7 seconds and the female for 1.3 seconds ($t = 7.13$: $p < 0.001$). The howl length of the two males in each group did not differ ($t = 0.734$: $p < 0.5$), but those of the Group P female were significantly longer than those of the female in Group V ($t = 3.386$: $0.001 < p < 0.01$).

With only one song analysed from each group it is impossible to confirm differences between groups. However, only males called Type 1 howls and each one was longer than any call by either adult female. Within each song, it is likely that as the adult female of Group P called throughout the song, she spent most time actually vocalising. In Group V the amount of time spent vocalising by the two adults during a song was always approximately equal.

3.5 The Properties of Indri Song

3.5.1 The Frequency of Calls and Groups of calls

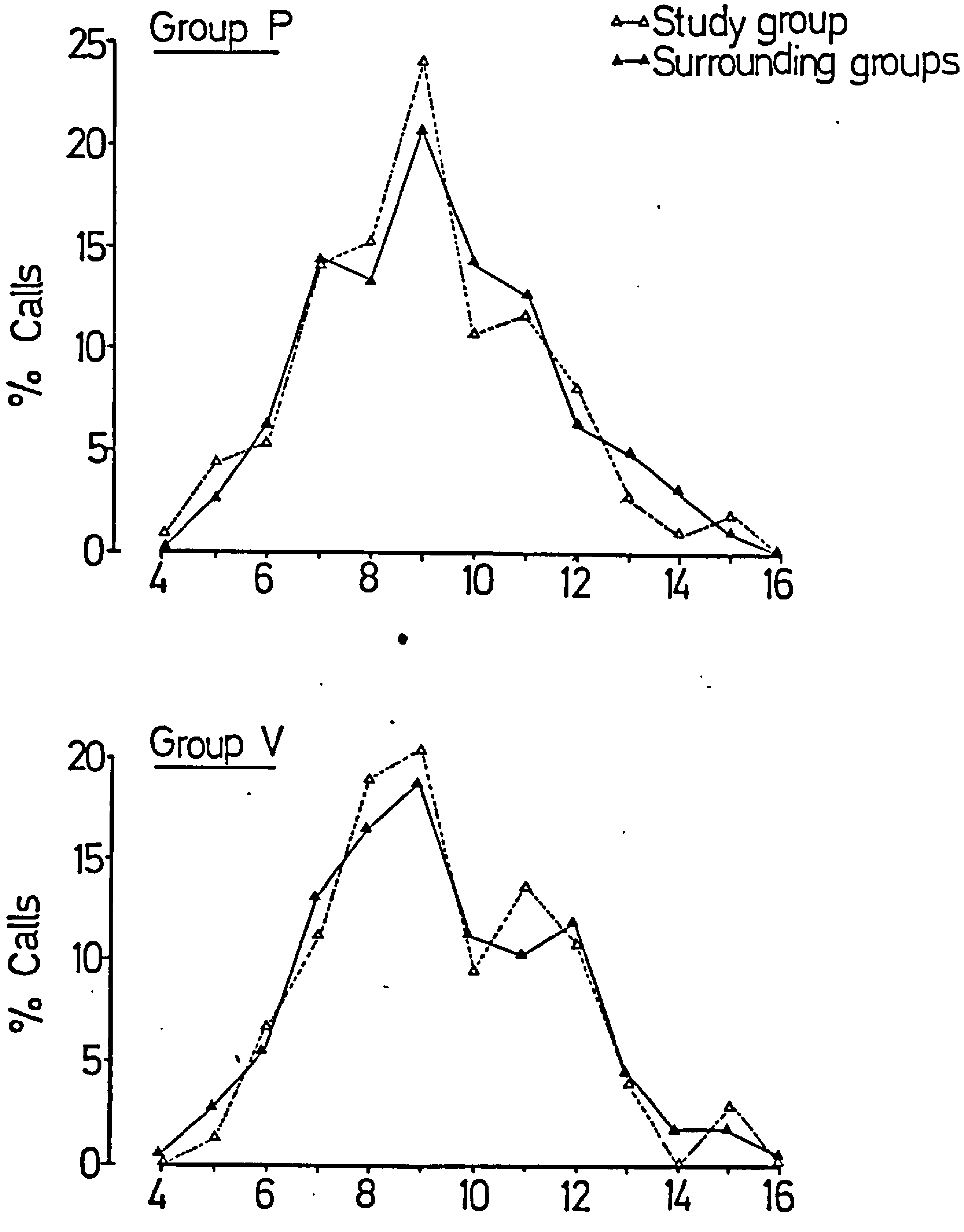
3.5.1.1 Temporal Distribution

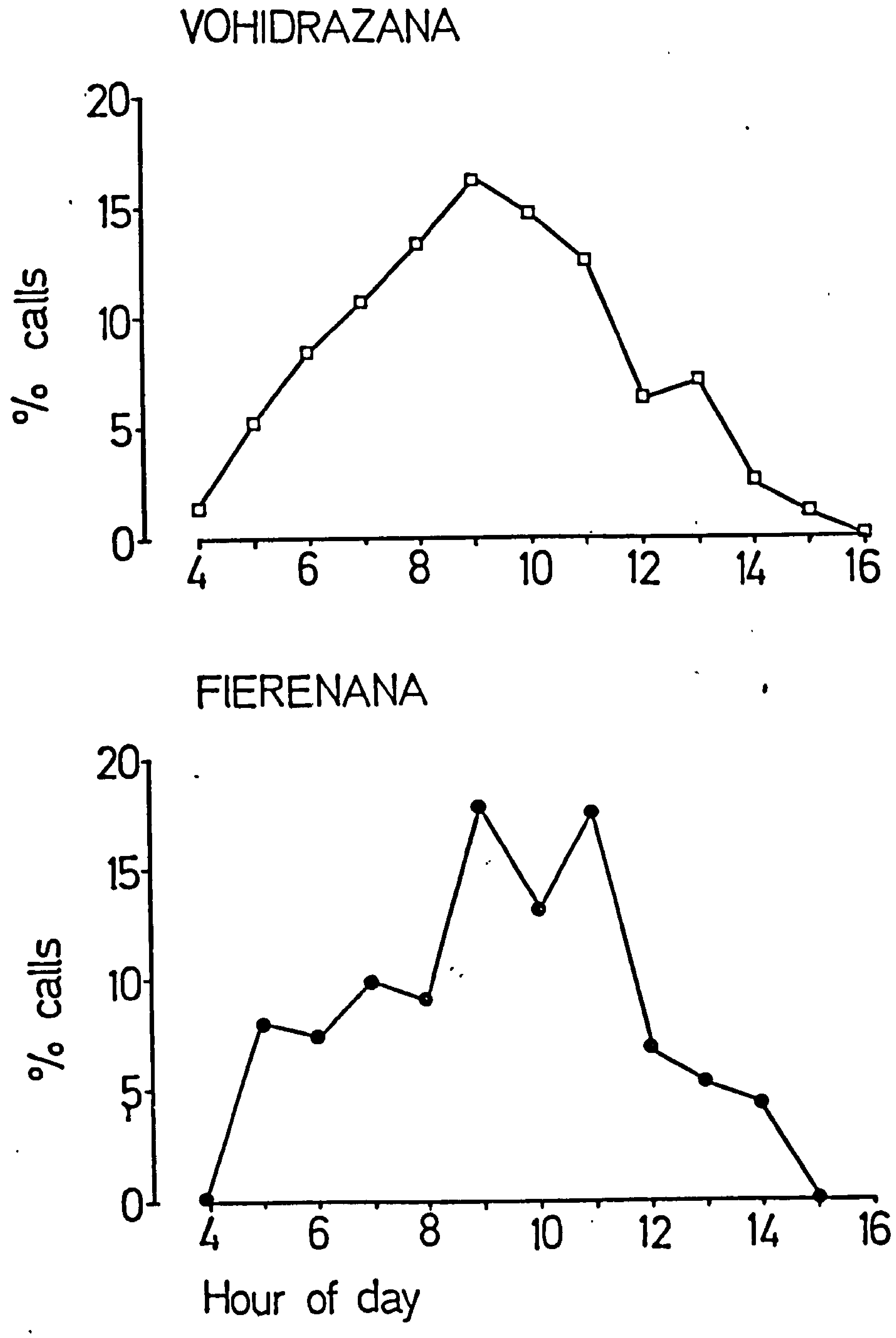
Over the whole year *Indri* calls were heard throughout the morning or early afternoon with a single peak at 0900 in all study areas (Fig. 9.5 ,Table 9.3). The slightly more spread distribution at Vohidrazana probably resulted from a better acoustic reception at the study position - the occasional late and early calls from distant groups being better perceived.

As *Indri* groups (by singing) induced other groups

Figure 9.5 Hourly distribution of *Indri* calls throughout the year. Call distributions of each study group and their local populations (Analamazoatra) and study populations at Vohidrazana and Fierenana are shown.

ANALAMAZOATRA




VOHIDRAZANA
% calls
20
15
10
5
0
4
6
8
10
12
14
16
FIERENANA
% calls
20
15
10
5
0
4
6
8
10
12
14
16
Hour of day

(1) ANALAMAZOATRA	
GROUP P	83.8%
GROUP P's LOCAL POPULATION	81.7%
GROUP V	85.2%
GROUP V's LOCAL POPULATION	82.0%
(2) VOHIDRAZANA	74.2%
(3) FIERENANA	74.3%

TABLE 9.3. The proportion of calls that occurred before 1300 hours each day.

to reply, successive calls were not independent of each other within any specified time period and hourly call frequencies could not, therefore, be statistically compared.

A call was considered to be part of a group or 'cluster' of calls if it (i) overlapped the call that started before it (0), (ii) started immediately the preceding call ended allowing time for sound transmission (I), or, (iii) started within 10 seconds of the end of the preceeding call (A). The 10-second limit beyond which subsequent calls were defined as being in a different 'cluster' was a natural one. The first calls of a new cluster generally commenced a few minutes or even hours after the last call of the preceding cluster.

As a cluster of calls appeared to be a natural group of calls, their timing was probably statistically independent of each other. The temporal distributions of call clusters ($X^2_{8df(max)} = 9.7432$: $0.2 < p < 0.3$) did not differ in the three study areas (Figure 9.6).

The percentage of calls that were 'single' calls (i.e. calls which were not preceded or followed by others from other groups according to the definition of a clustered call, above) did not vary greatly between Analamazoatra (23.4%), Vohidrazana (19.3%) and Fierenana (25.8%). The lower figure at Vohidrazana probably resulted from the better perception of distant calls (in the same cluster) by the observer in this study area. There appeared to be no variation between study areas in the temporal distribution of single calls (Figure 9.7).

Figure 9.6 Hourly distribution of groups of calls (call clusters) for each study area throughout the year.

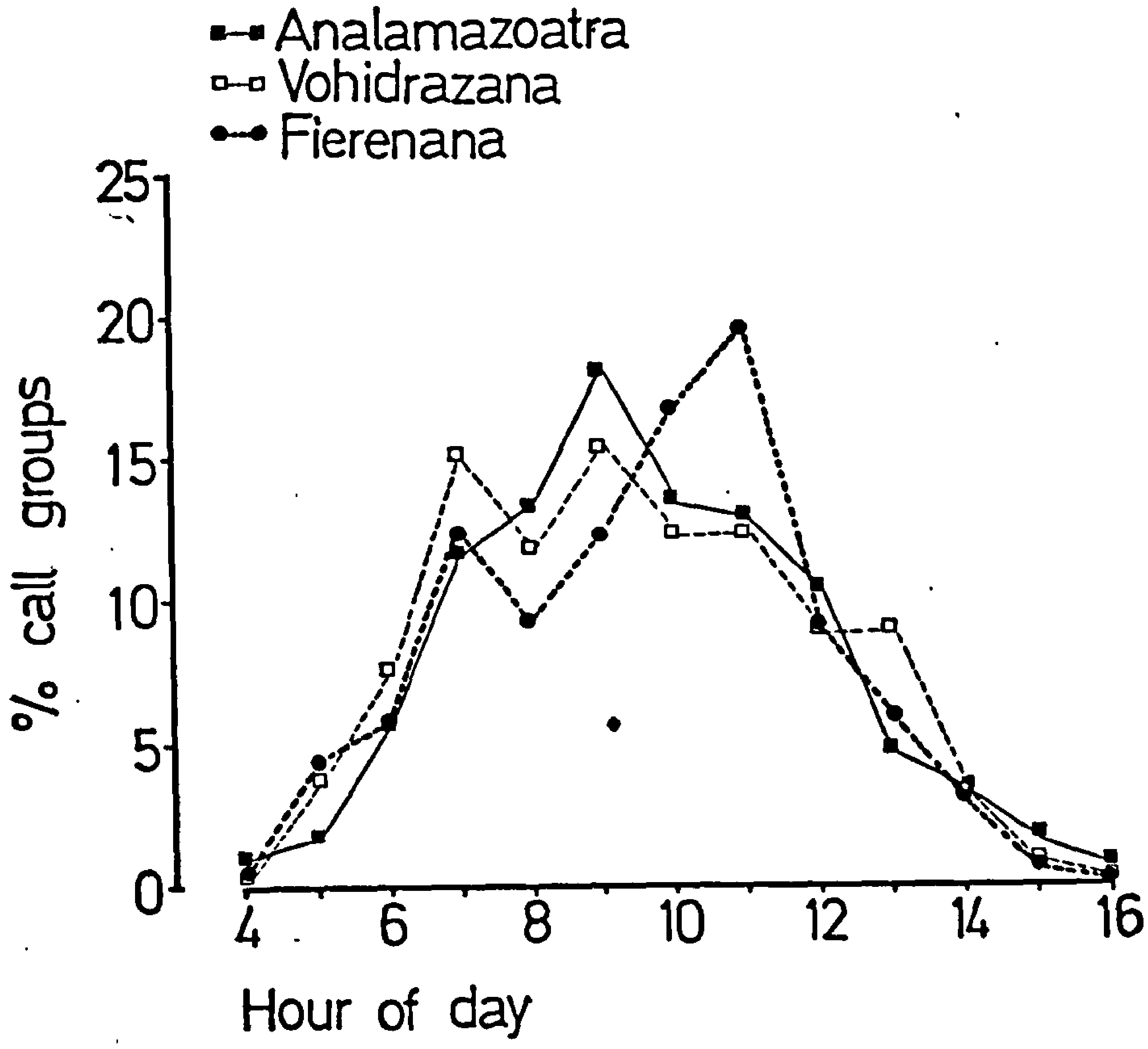
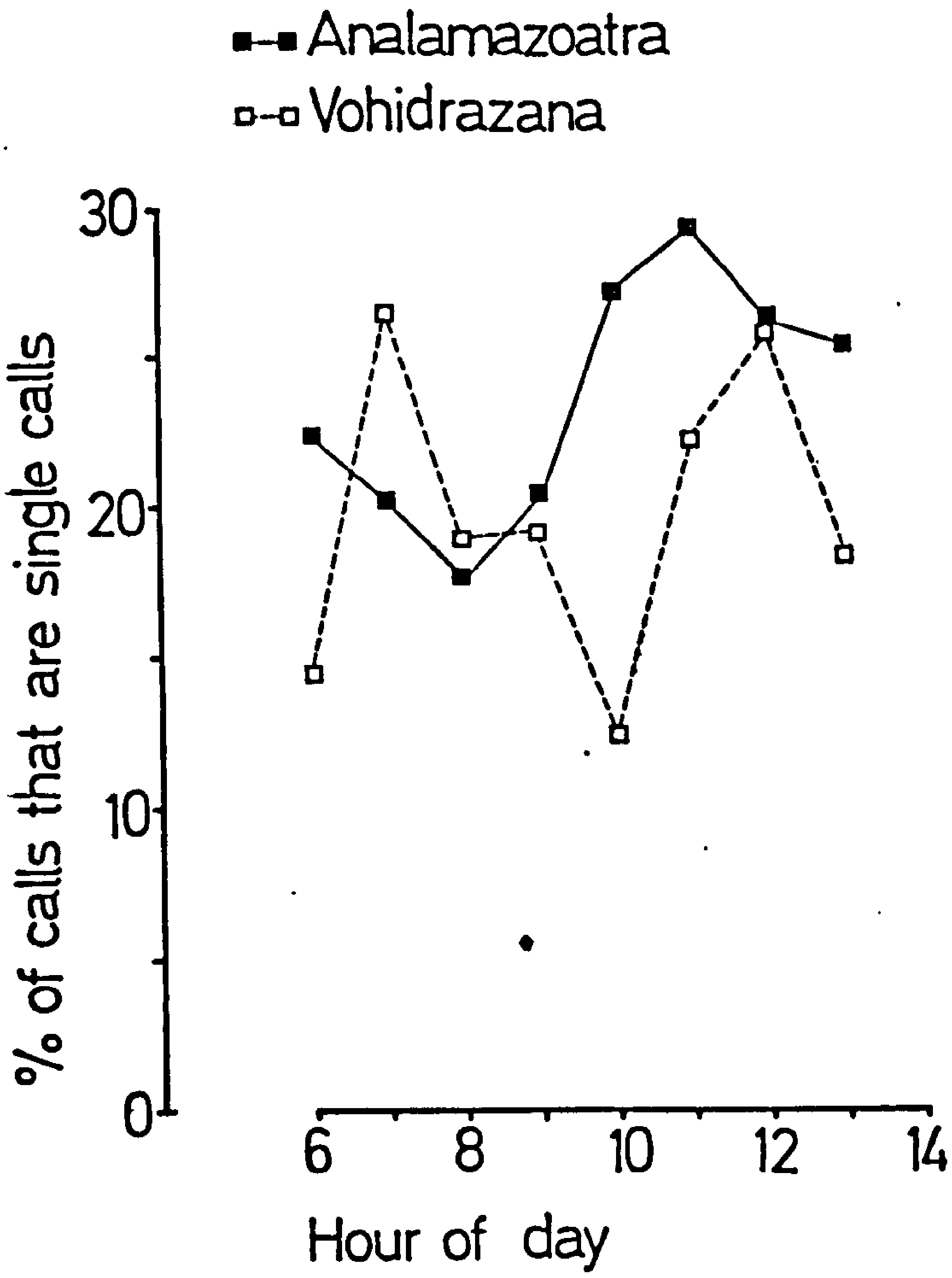

Analamazoatra
Vohidrazana
Fierenana
% call groups
25
20
15
10
5
0
4
6
8
10
12
14
16
Hour of day

Figure 9.7 Hourly distribution of "single" calls at Analamazoatra and Vohidrazana throughout the year.


■–■ Analamazoatra
□--□ Vohidrazana
% of calls that are single calls
30
20
10
0
6
8
10
12
14
Hour of day

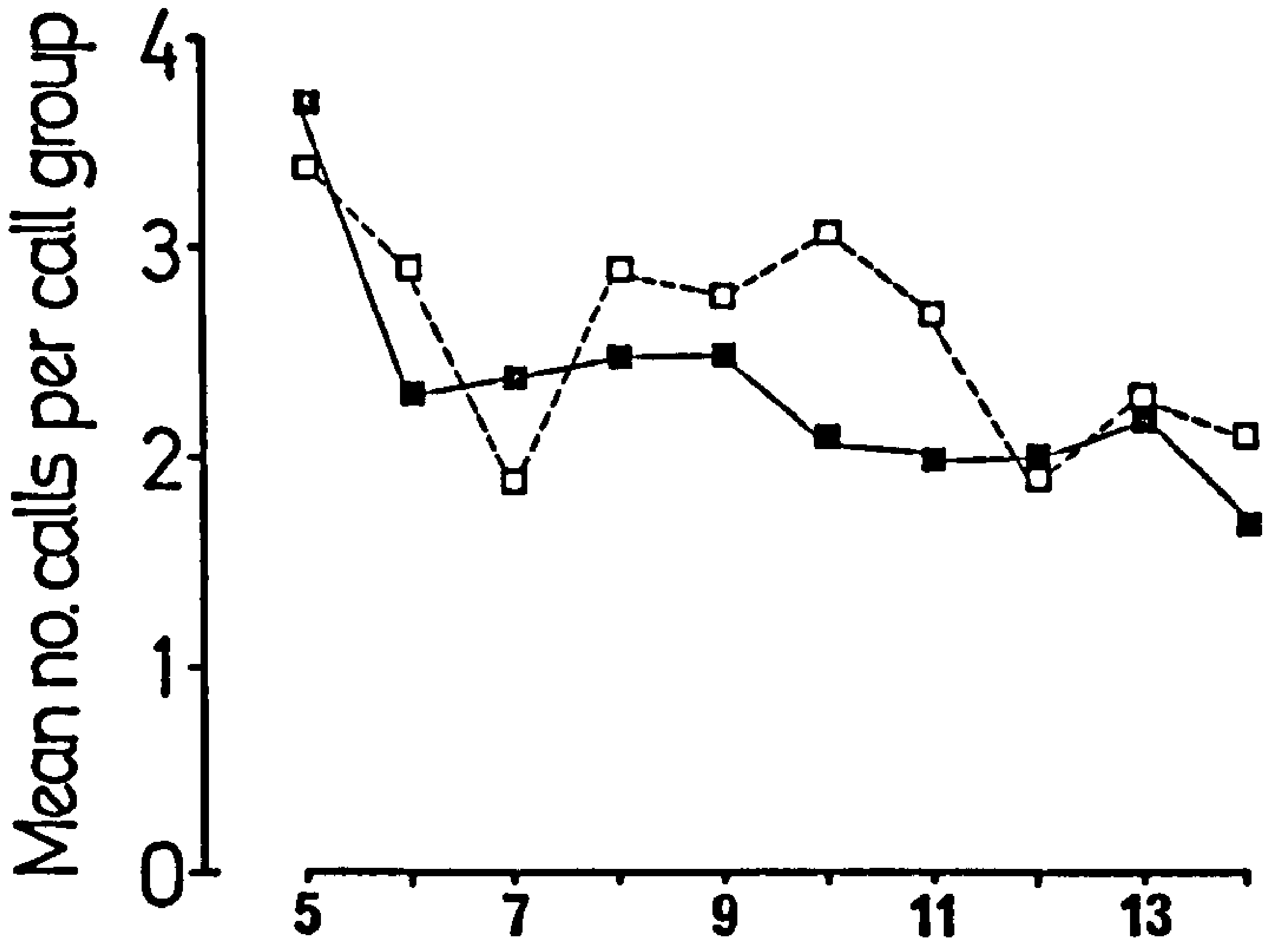
The mean number of calls in each cluster, although higher (for the reasons described above) and more variable at Vohidrazana, did not show any consistent pattern in its temporal distribtuion - although very early calls and very late calls would not normally be answered (Figure 9.8). A definite tendency for calls to occur in larger clusters in the morning than in the afternoon was present in both Analamzoatra and Vohidrazana (Figure 9.8). This was also evident when a more detailed analysis (Table 9.4) showed the , frequency of call clusters of various sizes for each hour of the day.

3.5.1.2 Seasonal Variation

The frequency and timing of *Indri* calls varied seasonally. The proportion of days in which the two study groups sang at least once increased gradually as the study progressed to peak during the mid-summer period (Circuits III and IV). In Figure 9.9 the discrepancies between the 2 study groups at the time of maximum calling were due either to the reduced calling in Circuit IV by Group V during the cyclone (which affected all activities) or to the large number of cohesion calls emitted by Group P when the adult female was wounded (see Chapter 8). It seems likely that, as the frequency of calling in the population peaked at Circuit III, the latter explanation is the correct one.

The frequencies of calls from the local populations

Figure 9.8 Hourly distribution of groups of calls (call clusters) throughout the year. (1) The mean number of calls in a group of calls are illustrated for Analamazoatra and Vohidrazana. (2) The difference between the percentage of calls and the percentage of groups of calls are shown for each hour of the day at Analamazoatra and Vohidrazana. Positive values indicate a preponderance of call clusters containing many calls. Negative values indicate a preponderance of call clusters containing few calls.


Mean no. calls per call group
4
3
2
1
0
5
7
9
11
13

1.


Analamazoatra
Vohidrazana
Difference between % calls and % call groups
+3
+2
+1
0
-1
-2
-3
4
6
8
10
12
14
16
Hour of day

2.

(1) VOHIDRAZANA

	NUMBER OF CALLS PER GROUP							
HOUR OF DAY	2	3	4	5	6	7	8	9+
4	-	-	-	-	-	-	-	1
5	2	-	1	1	1	-	1	2
6	6	4	1	1	1	1	3	2
7	12	6	4	3	2	1	4	2
8	6	3	4	-	2	2	1	2
9	7	6	5	2	2	3	1	3
10	10	6	4	5	-	-	1	5
11	8	7	4	-	3	-	-	-
12	8	6	1	3	2	-	-	-
13	8	8	1	-	1	1	-	1
14	3	1	-	-	1	-	-	-
15								
16								

TABLE 9.4. Hourly distribution of groups of calls of different sizes (call-cluster size) at Analamazoatra and Vohidrazana.

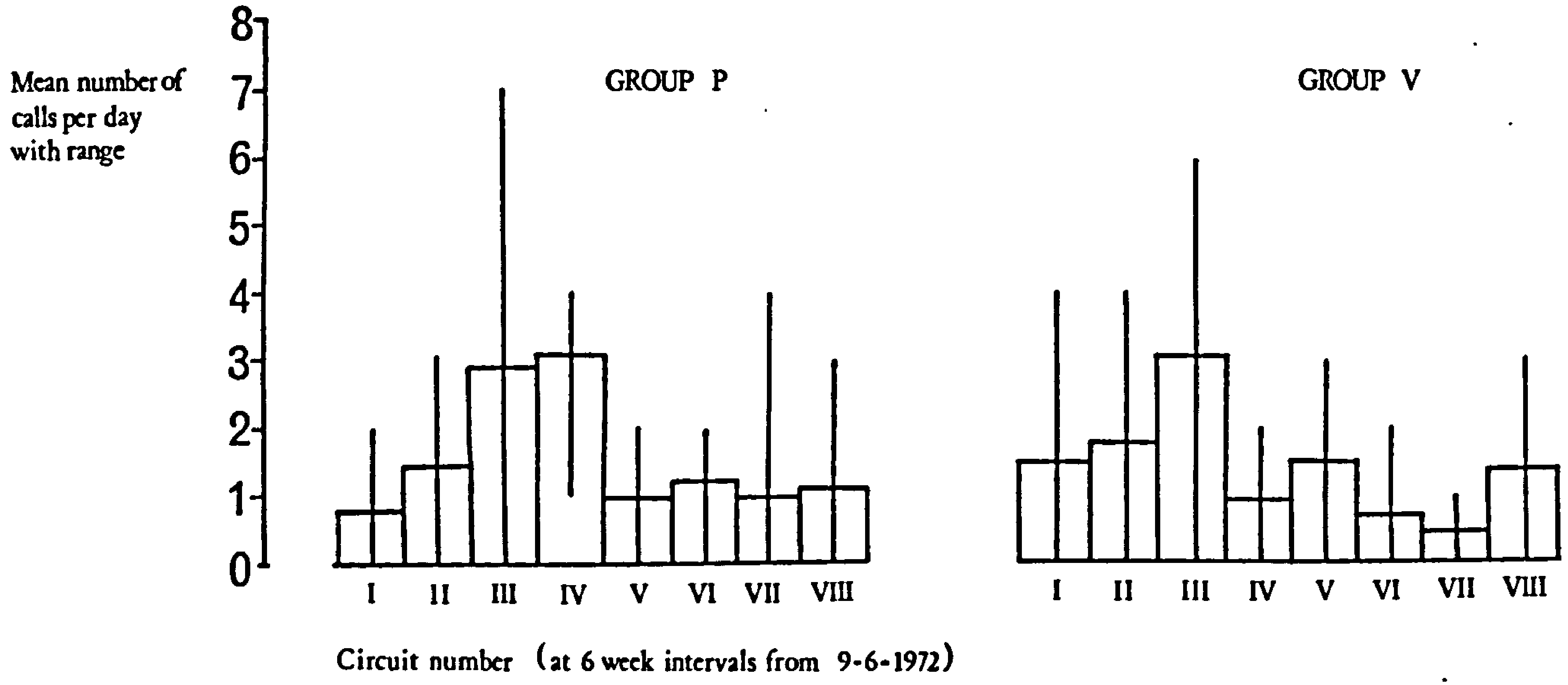
(2) ANALAMAZOATRA

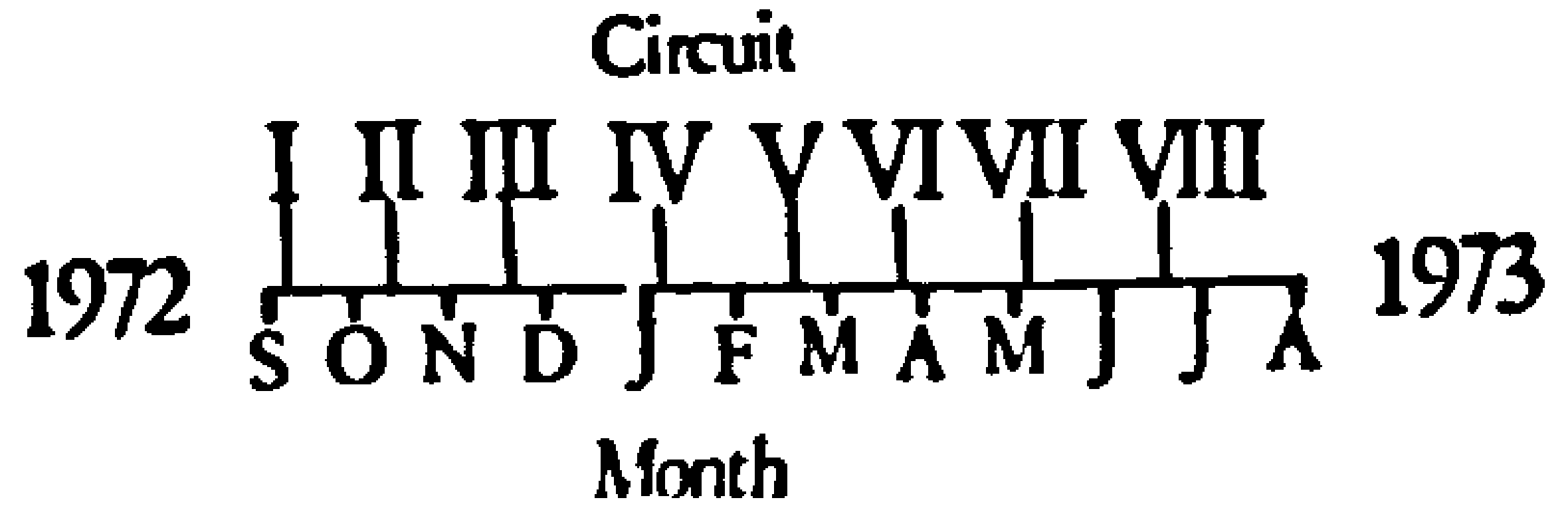
NUMBER OF CALLS PER GROUP

HOUR OF DAY	2	3	4	5	6	7	8	9+
4	1	-	-	-	-	-	-	-
5	2	1	-	1	2	-	2	-
6	3	8	3	2	2	-	-	1
7	20	4	6	5	5	2	1	1
8	11	13	10	11	4	1	1	1
9	24	13	9	4	1	6	0	6
10	9	15	7	2	0	1	1	3
11	16	6	5	6	2	2	0	1
12	19	3	6	3	3	0	0	0
13	3	9	2	1	-	-	-	1
14	8	1	2	-	-	-	-	-
15	2	-	3					
16								

TABLE 9.4. cont'd ...

Figure 9.9 Seasonal variation in the mean number of calls emitted daily by Group P and Group V.


Mean number of calls per day with range
0
1
2
3
4
5
6
7
8
GROUP P
GROUP V
I
II
III
IV
V
VI
VII
VIII
Circuit number (at 6 week intervals from 9-6-1972)


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
1973
Month

surrounding Group P and Group V differed. The numbers of calls by Indri groups near to Group V exceeded those near to Group P (Figure 9.10), at times of high overall calling frequency but not at other times of the year. There was no reason to consider auditory perception to be superior or animal density greater around Group V's home range than around Group P.

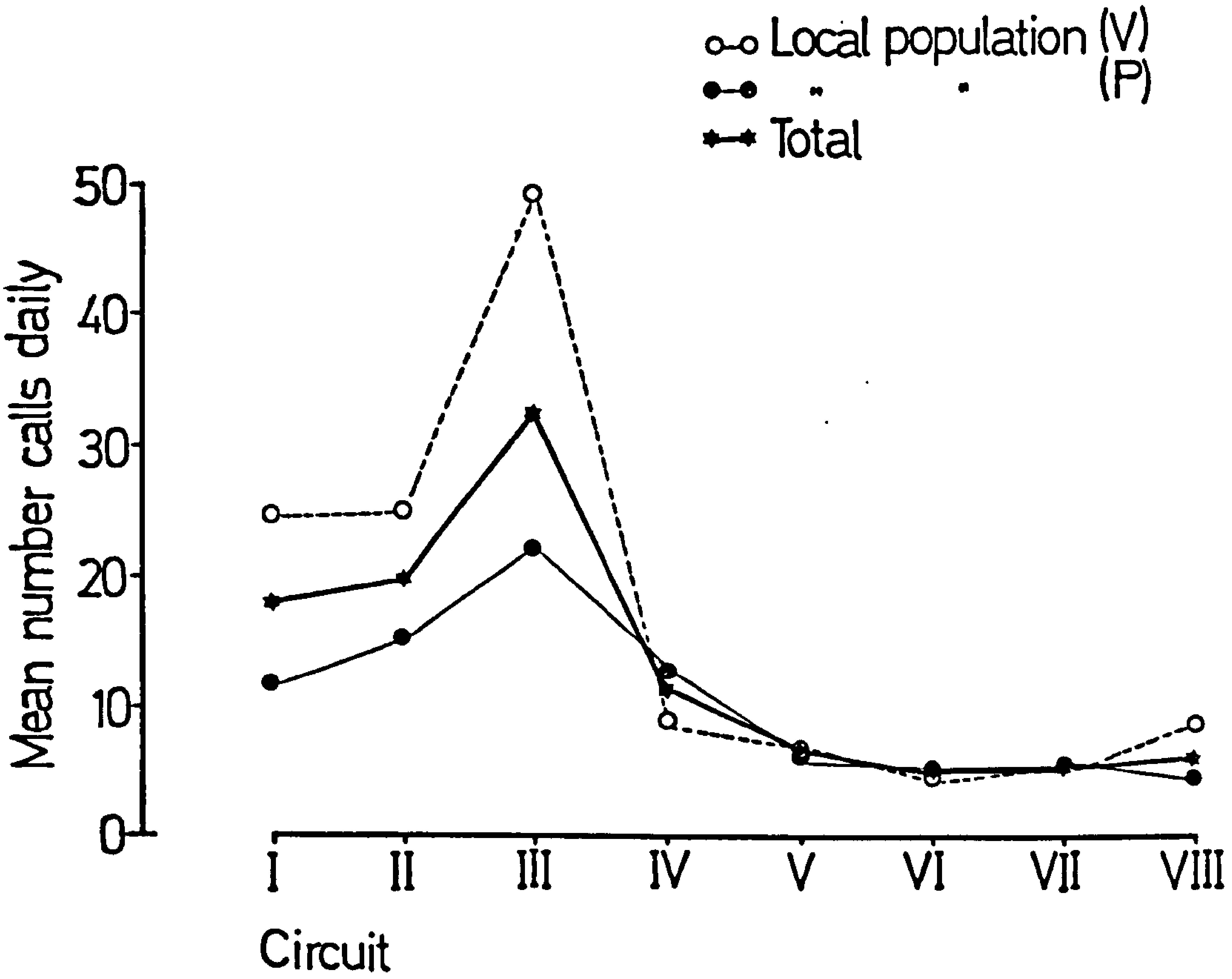
Calling frequency was too variable for seasonal distributions of calls to be compared in the other two study areas, which were visited only for 3 days every 6 weeks. The same seasonal trends however, appeared to be present (Figure 9.11), at Vohidrazana.

Due to the large number of calls around Group V, the percentage contribution by this group to the number of calls emitted by the population was inferior to that of Group P (Figure 9.12). Both study groups contributed most to the population's calls at times of low general calling activity.

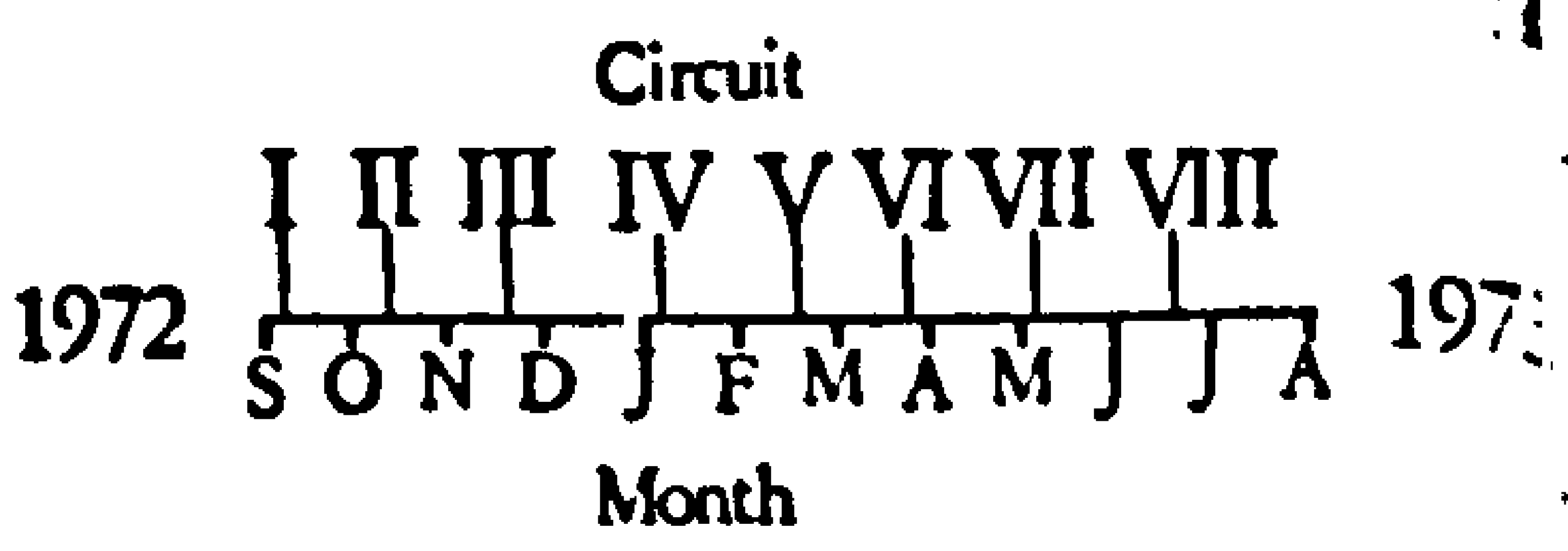
The duration of calls did not appear to vary greatly (see Section 3.5.2) as distributions over the year of the total number of minutes during which calls were heard and the frequency of calls were very similar. (Figure 9.13).

Seasonal variation in the timing of calls varied with seasonal changes in the activity period (Chapter 3). Calls started earlier and continued later in the austral summer (Circuits III and IV) when most calls were heard and Indri were active longest (Table 9.5). The possibility that a simple relationship existed

Figure 9.10 Seasonal variation in the mean number of calls emitted daily by local populations of each study group at Analamazoatra.

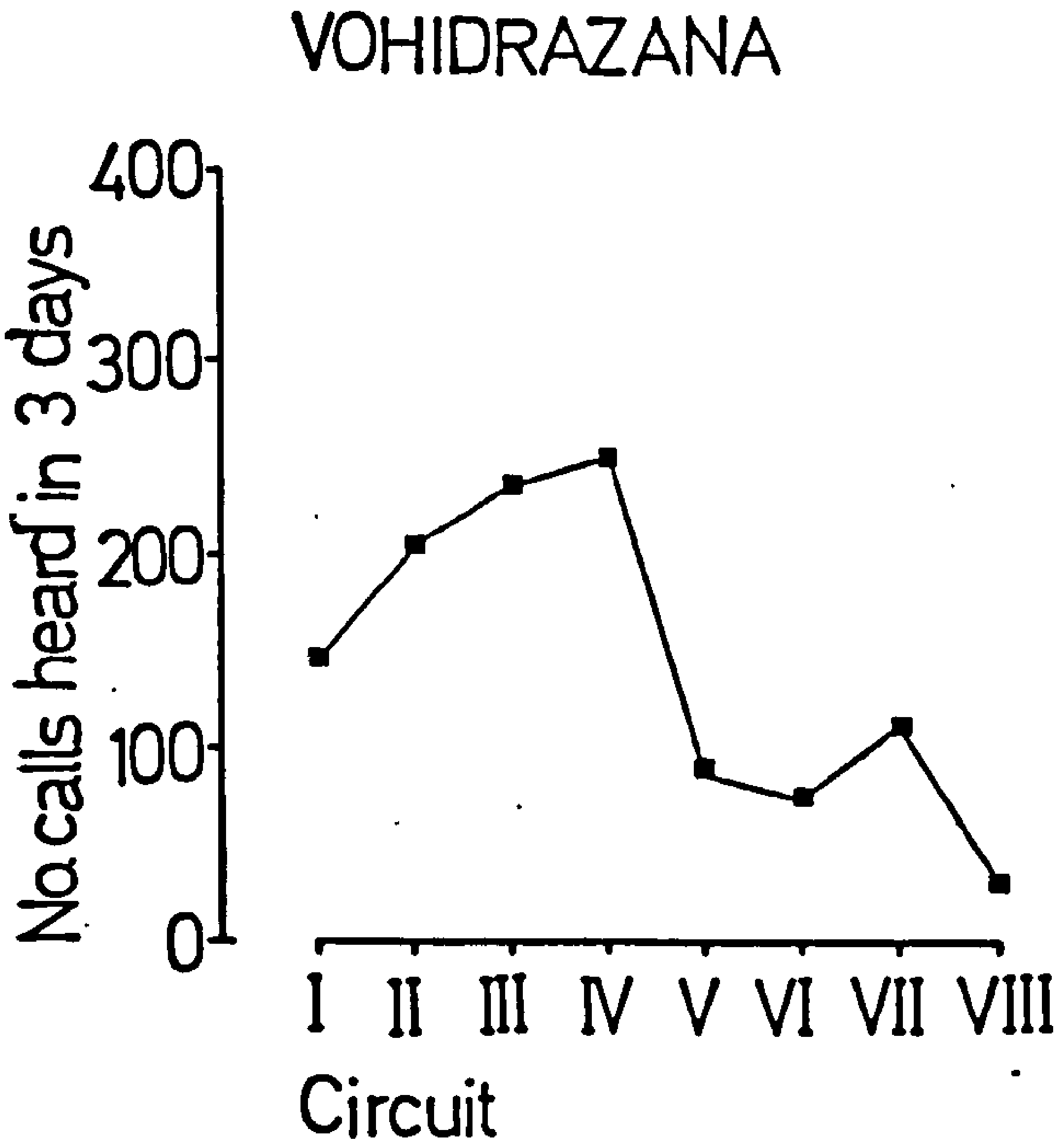


o–o Local population (V)
●–● " " (P)
★–★ Total
Mean number calls daily
50
40
30
20
10
0
I
II
III
IV
V
VI
VII
VIII
Circuit



Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
197
Month

Figure 9.11 Seasonal variation in the number of calls heard at Vohidrazana during each 3 day period of observations.


VOHIDRAZANA
No. calls heard in 3 days
400
300
200
100
0
I
II
III
IV
V
VI
VII
VIII
Circuit

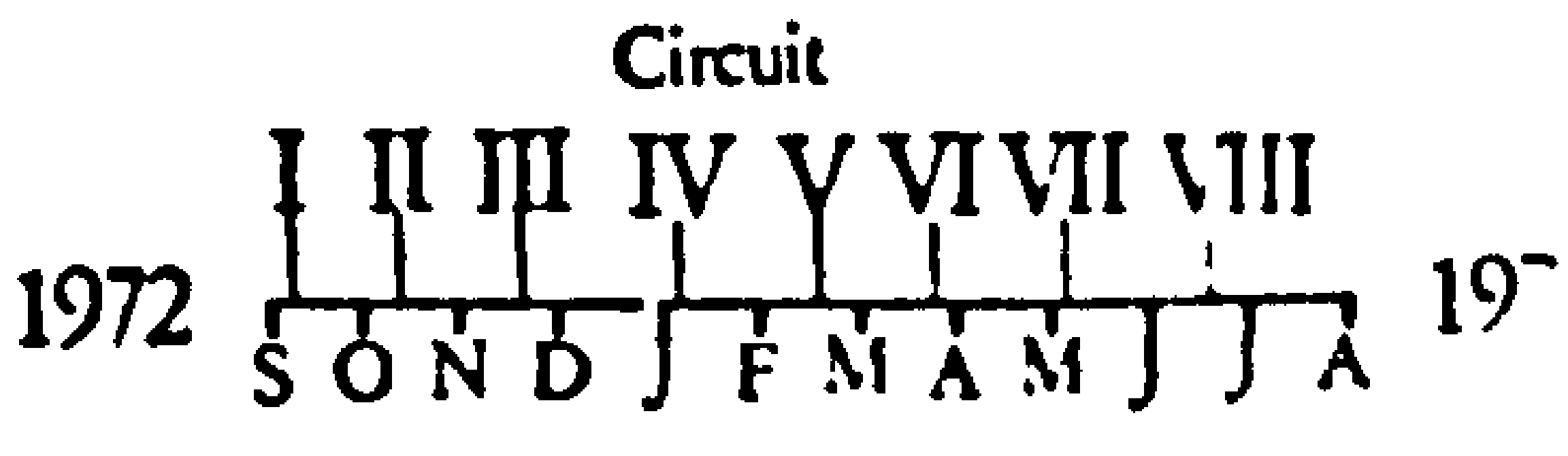
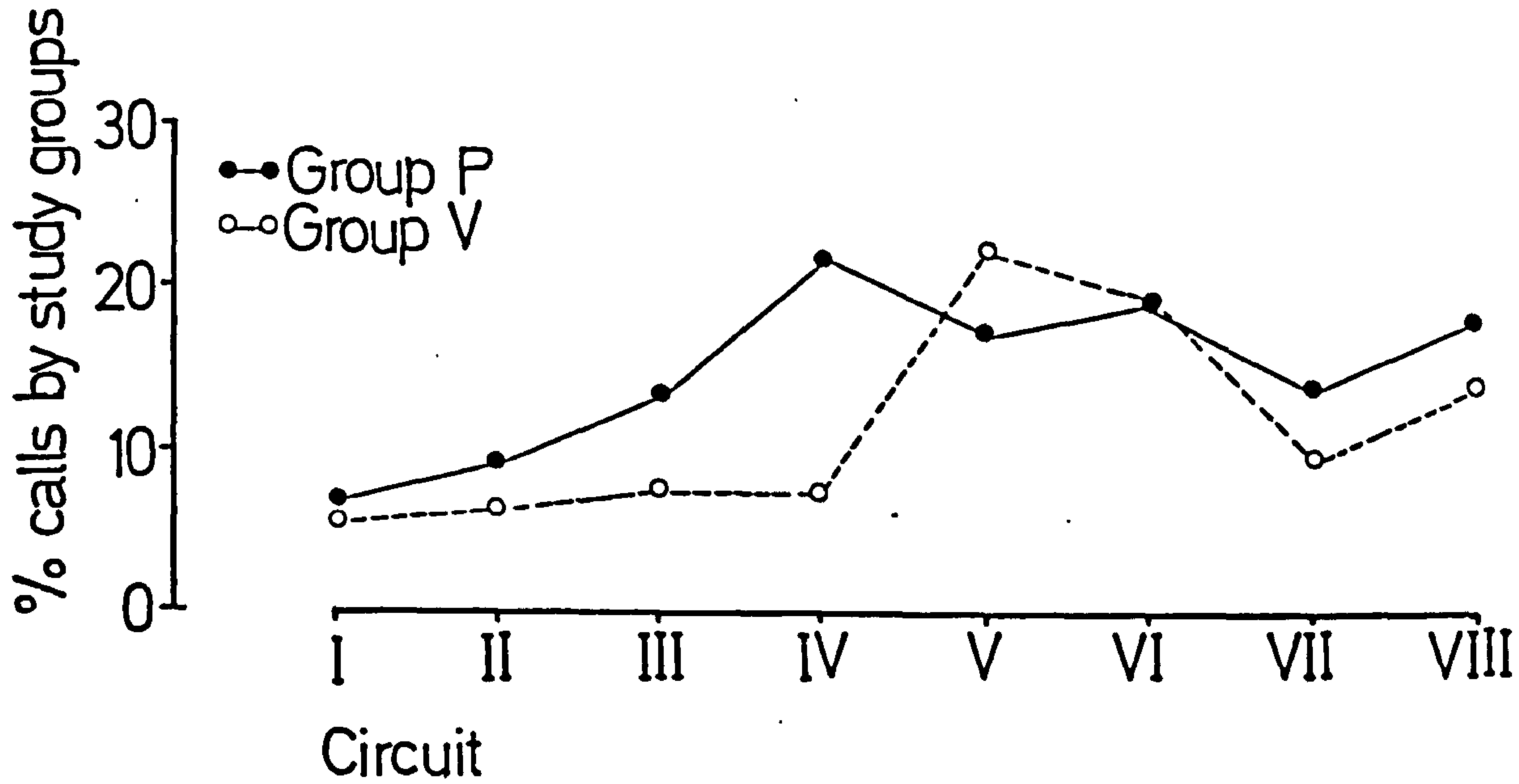

Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
19
Month

Figure 9.12 Seasonal variation in the proportion of calls heard in their local population that were emitted by each study group.


% calls by study groups
30
20
10
0
Group P
Group V
I
II
III
IV
V
VI
VII
VIII
Circuit

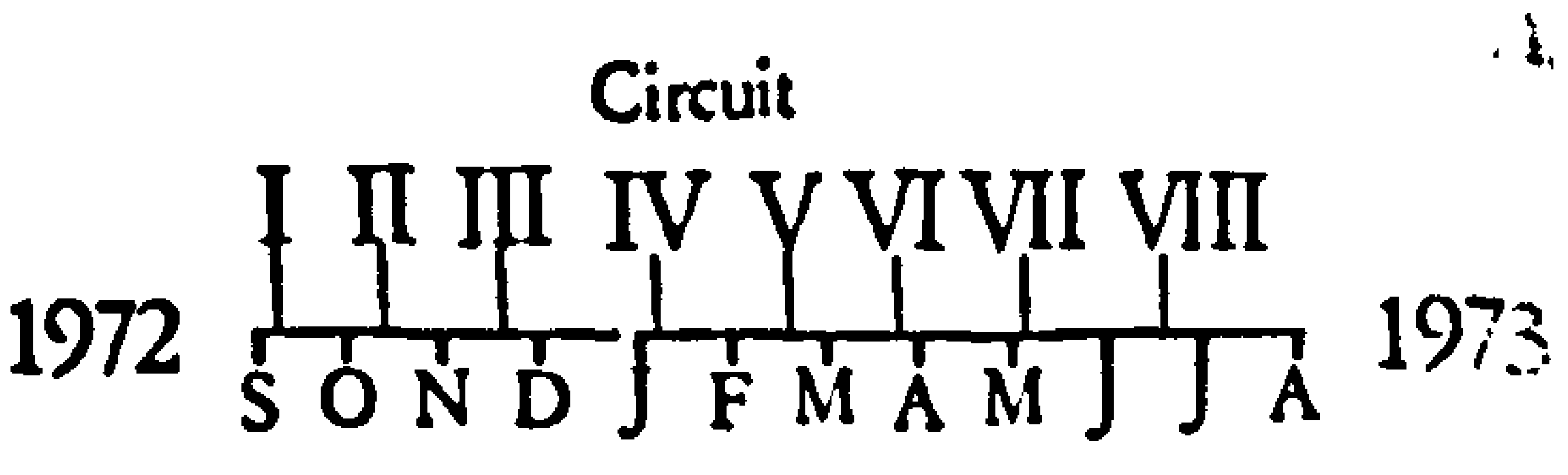
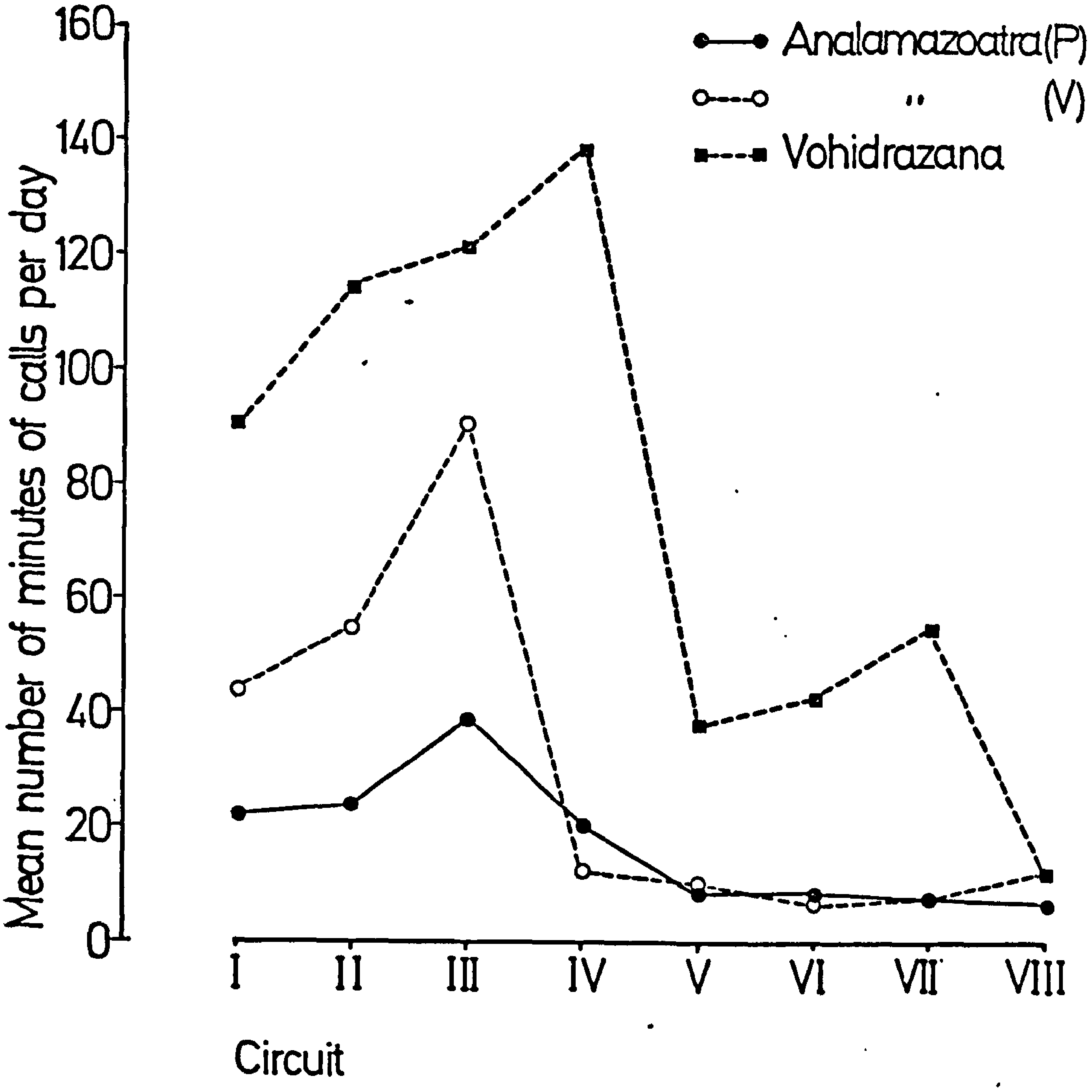
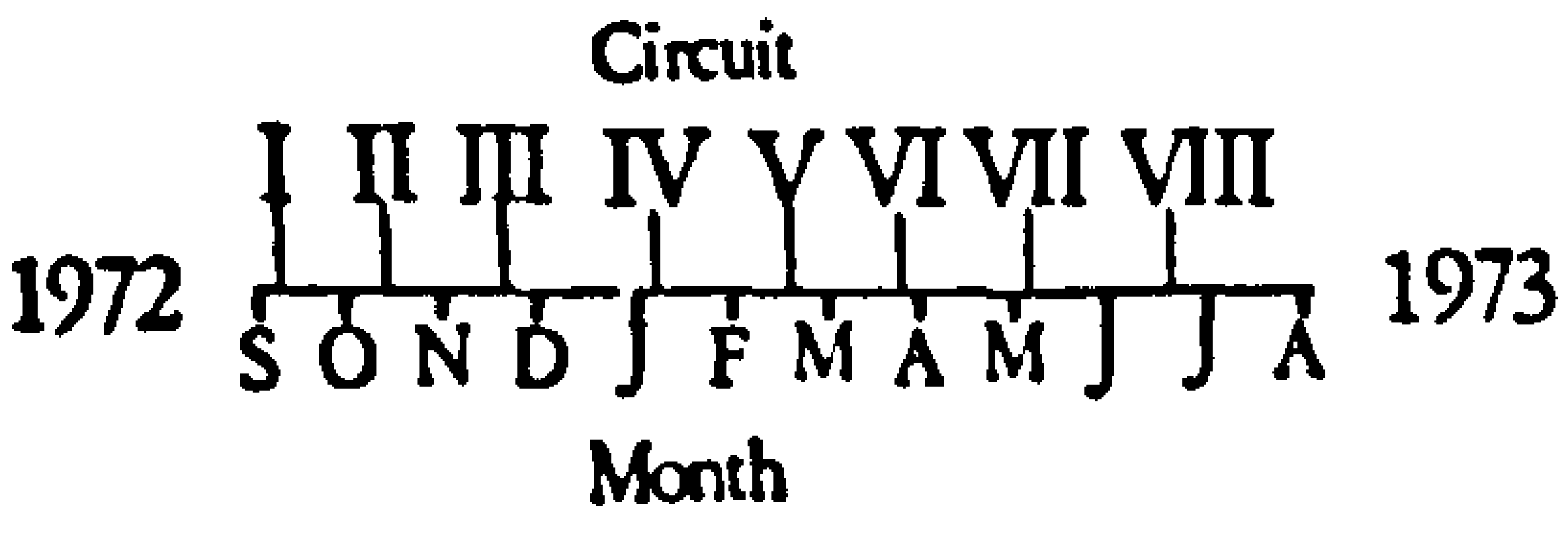

Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
1973
Month

Figure 9.13 Seasonal variation in the mean number of minutes of calls emitted daily by each study group's local populations at Analamazoatra, and at Vohidrazana.


Analamazoatra(P)
" (V)
Vohidrazana
Mean number of minutes of calls per day
160
140
120
100
80
60
40
20
0
I
II
III
IV
V
VI
VII
VIII
Circuit


Circuit
I II III IV V VI VII VIII
1972
S O N D J F M A M J J A
1973
Month

(1) VOHIDRAZANA

HOUR OF DAY

CIRCUIT	I	II	III	IV	V	VI	VII	VIII
4	-	-	6.8	-	-	-	-	-
5	-	-	22.9	1.6	-	-	-	-
6	-	-	11.0	24.7	5.6	3.9	-	-
7	-	6.8	8.5	16.7	27.8	-	15.3	20.0
8	31.1	14.6	6.8	6.8	20.0	2.6	14.4	26.7
9	16.9	18.0	9.7	11.2	17.8	36.8	25.2	6.7
10	23.0	14.6	11.4	10.0	5.6	23.7	24.3	10.0
11	14.2	21.5	4.2	9.2	6.7	25.0	10.8	30.0
12	7.4	3.4	3.4	10.4	6.7	6.6	9.0	3.3
13	7.4	8.3	11.0	7.6	7.8	-	0.9	3.3
14	-	7.8	3.4	1.6	1.1	1.3	-	-
15	-	4.9	0.4	0.4	1.1	-	-	-
16	-	-	0.4	-	-	-	-	-

TABLE 9.5. Seasonal variation in the hourly distribution of calls at Analamazoatra and Vohidrazana (% of calls occuring in each hour of the day).

(2) ANALAMAZOATRA

HOUR OF DAY

CIRCUIT	I	II	III	IV	V	VI	VII	VIII
4	-	-	1.0	0.5	1.0	-	-	-
5	-	0.7	6.8	4.8	-	-	-	-
6	1.5	4.3	9.9	15.6	-	-	-	-
7	16.2	17.5	8.2	23.7	14.7	18.6	3.6	3.9
8	20.1	13.9	13.0	11.8	10.8	11.6	23.8	26.2
9	23.5	18.8	18.1	7.0	23.5	17.4	36.7	24.3
10	17.4	16.2	7.2	7.0	18.6	29.1	11.9	15.5
11	16.2	10.9	14.0	5.9	15.7	16.3	14.3	16.5
12	12.0	10.9	7.4	11.3	10.8	4.6	-	7.8
13	1.5	4.9	6.6	4.3	2.0	1.2	10.7	3.9
14	1.2	2.0	3.7	4.8	2.0	-	-	1.9
15	0.4	-	2.9	3.2	1.0	1.2	-	-
16	-	-	1.0	-	-	-	-	-

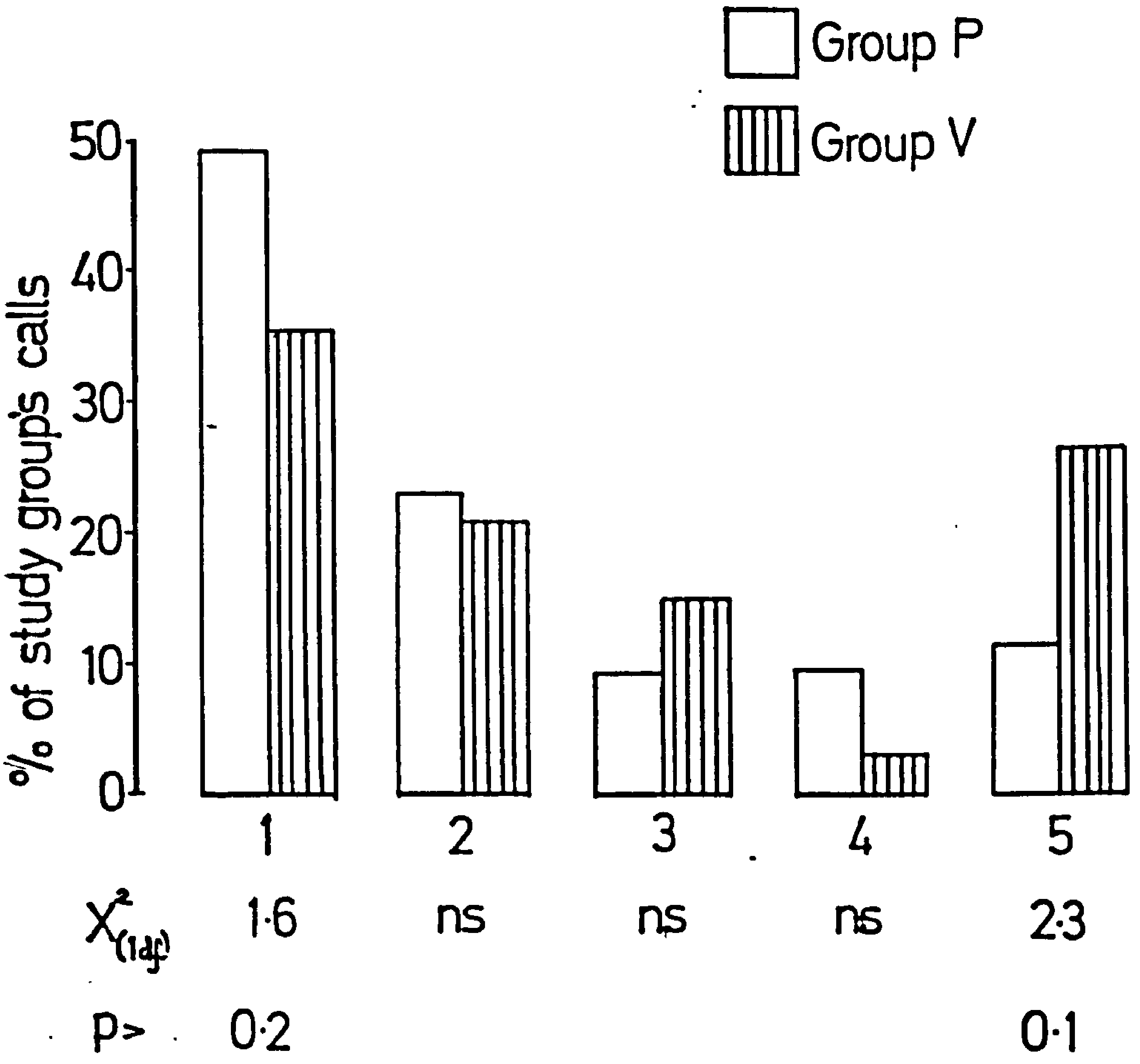
TABLE 9.5. cont'd ...

between the time of onset of calls from the population and the time of onset of calls from the study groups was examined (Figure 9.14), but the few data available did not reveal differences between the study groups.

3.5.1.3. Call Cluster Size

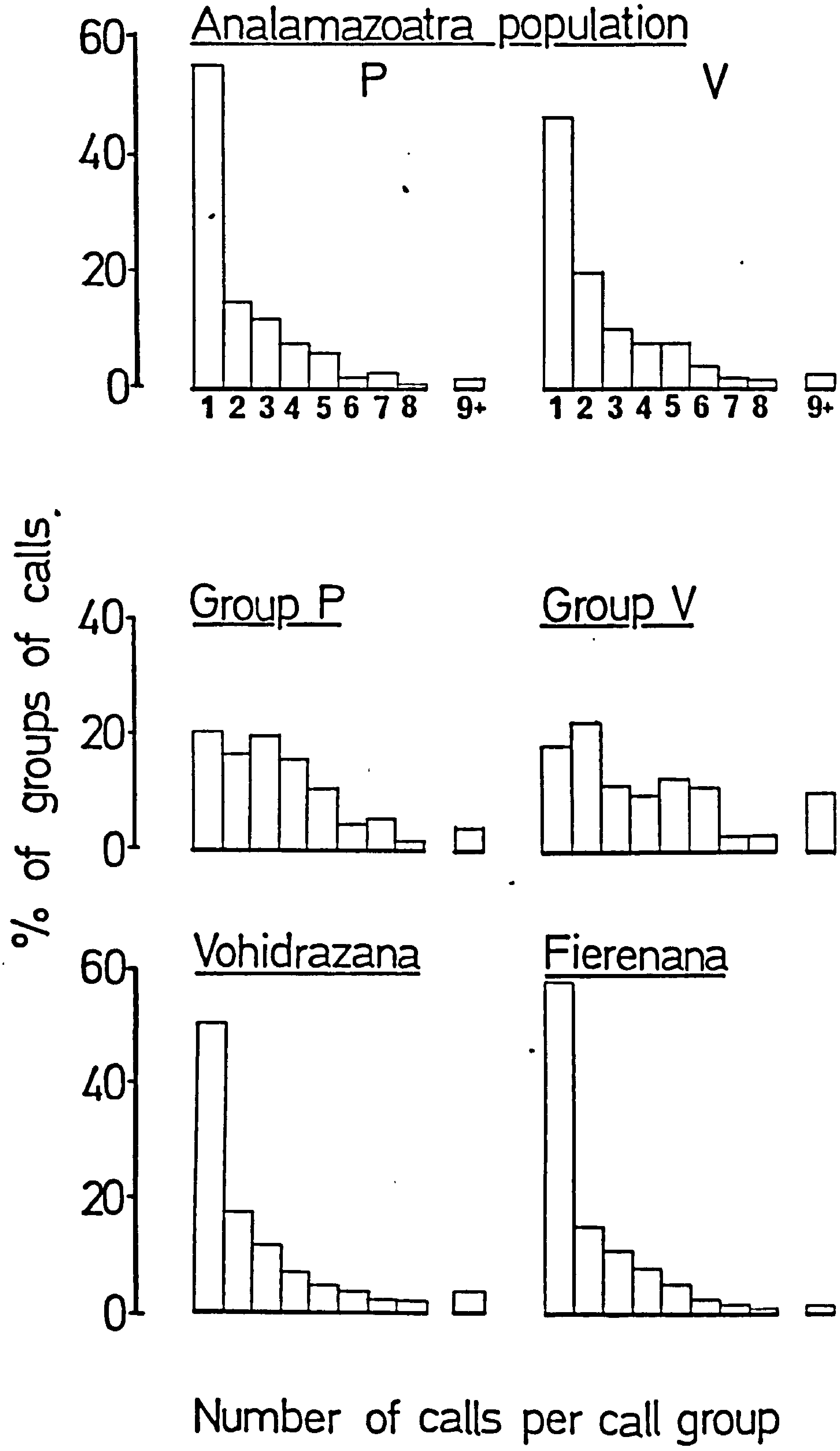
The sizes of clusters of calls were not directly comparable between study areas as the observer's sensitivity to distant calls varied according to his position (Figure 9.15). It is unlikely that both the main study groups were atypical in their involvement in clustered calls and it is probable therefore, that the large number of single calls heard in the population were, in fact, replies to distant groups whose calls could not be heard by the observer. Categories of call cluster size were defined in order to obtain sufficient numbers for statistical tests. The participation of the two study groups and their local populations in call clusters of each size category were then compared (Table 9.6). Although the two study groups did not differ in this measure ($X^2_{3df} = 6.208 : 0.1 < p < 0.2$), their local populations did ($X^2_{3df} = 7.895 : 0.02 < p < 0.05$). These inter-population differences could be attributed to the proportion of calls that were not answered and were not themselves answers i.e. single calls ($X^2_{1df} = 5.022 : 0.02 < p < 0.05$). As it is very unlikely that the observer could hear calls in one part of this forest better than in another there appeared to be more 'two-way' communication in the local population surrounding

Figure 9.14 Relationship between the timing of first calls in the local population and the timing of the study group's first calls in the morning. Categories of time (in minutes) separating calls in the population from calls by the study groups are illustrated with the results of tests between groups where they differed most.



1 = 1st call in population emitted by study group
2 = " " " precedes group's 1st call by 1'–50'
3 = " " " " " " 51'–100'
4 = " " " " " " 101'–150'
5 = " " " " " " >150'

<u>Figure 9.15</u> The proportion of calls by each study group, their local population and groups in other study areas, that occurred in call-clusters of different sizes.


Analalamazoatra population
P
V
Group P
Group V
Vohidrazana
Fierenana
% of groups of calls
60
40
20
0
1 2 3 4 5 6 7 8 9+
Number of calls per call group

	STUDY GROUPS		STUDY GROUPS' POPULATIONS	
CALL CLUSTER SIZE	P	V	P	V
1	24	14	204	152
2	21	17	54	65
3-5	52	23	92	81
5+	16	19	20	28
X^2_{3df}	6.2081		7.8950	
p	$0.1<p<0.2$		$0.02<p<0.05$	

TABLE 9.6. Differences in participation in groups of calls of various sizes (call cluster size) between (1) the main study groups and (2) the main study groups' local populations.

Group V than that surrounding Group P.

3.5.1.4 Daily Variation in Calling Frequency

The numbers of calls heard within each Circuit varied widely from day to day (Table 9.7). To at least some extent, this depended on the state of the weather as cold, wet and windy conditions appeared to inhibit calling. On days with sporadic, hard rain, *Indri* would move, feed and call between showers. For Group P's local population, the effect of rain was investigated by dividing up the observations into (i) Dry days (rain falling 0-5% of the time), (ii) Slightly wet days (rain falling 12-30% of the time) and (iii) Very wet days (when rain fell at least 37% of the time). The results (Table 9.8) showed that heavy rain (or conditions associated with rain) affected the number of calls emitted each day, the mean number of call clusters each day, but not the mean number of calls in each cluster.

The mean daily number of calls did not, however, reduce in *proportion* to the amount of time that the rain fell, as *Indri* compensated by calling relatively more during bright intervals in the weather.

The two study groups did not differ in the number of days in which they called at least once ($X^2_{1df}=0.509$: $0.3 < p < 0.5$) and neither did the numbers of calls they emitted each day greatly differ (Figure 9.16).

3.5.2 The Duration of Indri Calls

Each song by a group of *Indri* may last from 45

(1) Group P's ANALAMAZOATRA

OBSERVATION DAY NUMBER

CIRCUIT	I	II	III	IV	V	VI	VII	VIII	
P11	-	14	35	12	-	1	25^4	4^2	
P10	-	22^2	21^1	9^2	3^1	11^2	10^1	2	
P9	-	13^1	26^2	12^3	9^2	4	3^1	6	
P8	-	7^1	31^3	10^2	3^1	9^2	5	6^1	
P7	14^1	3	26^7	21^4	10^1	8^1	1	7^1	
P6	14^2	26^2	12^2	19^4	6^2	9^2	1	3^1	
P5	11^1	19^2	13^2	10^2	5^1	2	4^1	8	
P4	9^1	21^2	18^3	7^3	12^1	1	1	10^2	
P3	14^0	17^3	23^2	16^4	12^2	5^1	2	7^1	
P2	9^1	9^1	16	12^4	3	7^3	5^1	1	
TOTAL	71^5	151^{14}	221^{30}	128^{28}	63^{11}	57^{11}	57^8	44^8	792^{115}
% of popn.	7.1	9.3	13.5	21.8	17.5	19.3	14.0	18.2	14.5%

N^x : x = no. of study groups' calls

N = no. of calls heard in local population

$$\text{P mean no. calls/day} = \frac{POP_n}{10.3} \quad \frac{P}{1.5}$$

TABLE 9.7. Daily variation in numbers of calls heard.

(2) <u>Group V's ANALAMAZOATRA</u>

	CIRCUIT	I	II	III	IV	V	VI	VII	VIII	
OBSERVATION DAY NUMBER	V7	58^4	33^4	25^3	11^1	4^2	7^2	4	14^1	
	V6	14	24	55^3	14^1	9	2	10^1	3	
	V5	25^1	31^2	57^4	9	4^1	2	2^1	11^3	
	V4	15^2	38^3	64^5	7^1	8^1	7^2	6^1	3	
	V3	26^3	20^1	57^5	3	11^3	4	3	15^2	
	V2	9	3	36^3	10^1	4^2	4^1	6	4^1	
	TOTAL	193^{11}_{*}	149^{10}	294^{23}	54^4	40^9	26^5	31^3	50^7	837^{72}
	% of pop^{n}.	5.7	6.8	7.8	7.4	22.5	19.2	9.7	14.0	8.6%

* 8 days data.

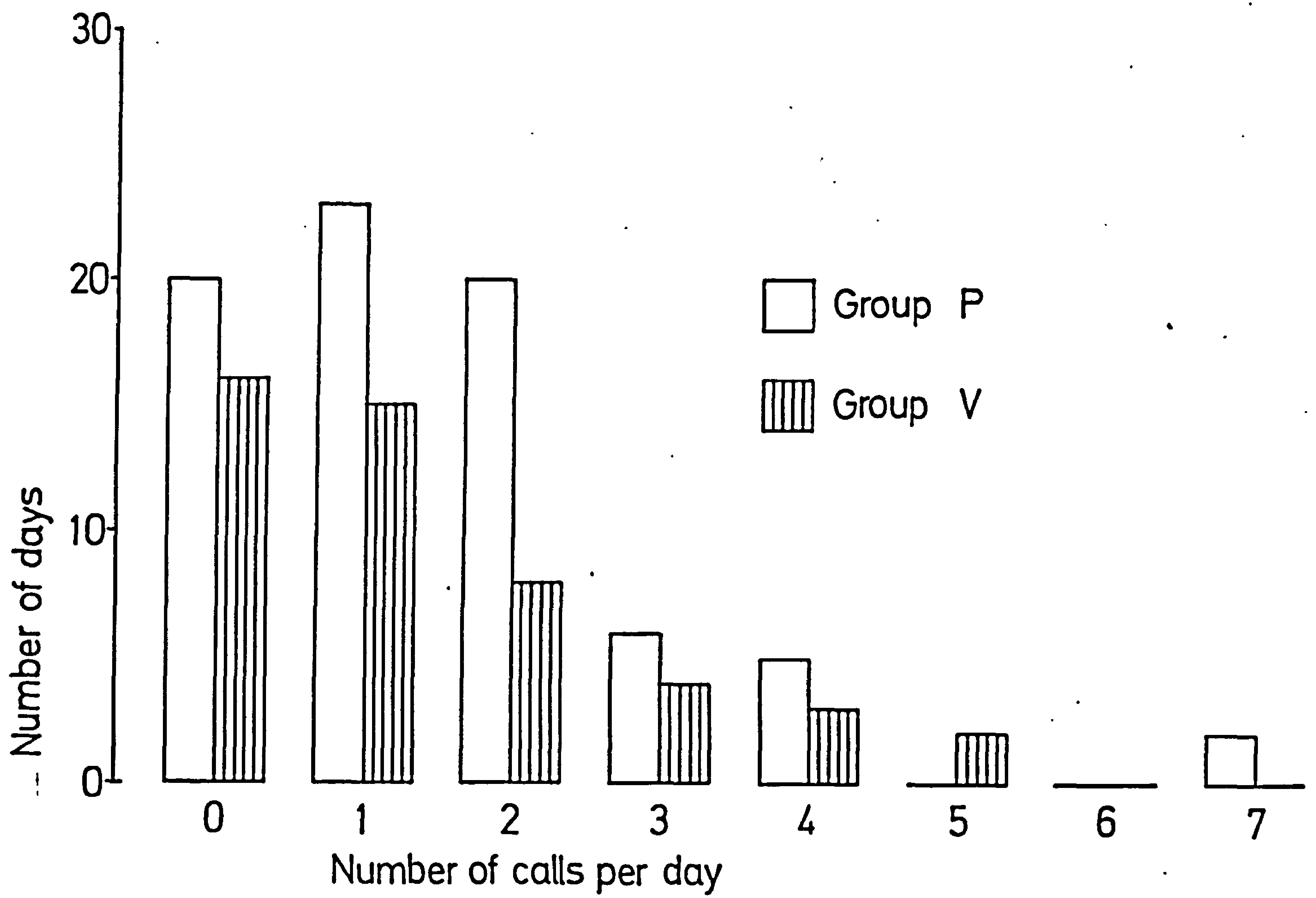
V mean no. calls/day = $\frac{POP_n}{16.7} \quad \frac{V}{1.4}$

TABLE 9.7. Daily variation in numbers of calls heard (cont'd)

	DRY	SLIGHTLY WET	VERY WET
sample:	15 days	14 days	10 days
no. calls/day	12.7	12.3	7.7
no. clusters/ day	5.5	5.2	3.4
$\bar{X}$ calls/ clusters	2.3	2.4	2.2

TABLE 9.8. The effect of weather on calling frequency at Analamazoatra.

Figure 9.16 The numbers of calls emitted daily by Group P and Group V throughout the year.


30
20
10
0
Number of days
0
1
2
3
4
5
6
7
Number of calls per day
Group P
Group V

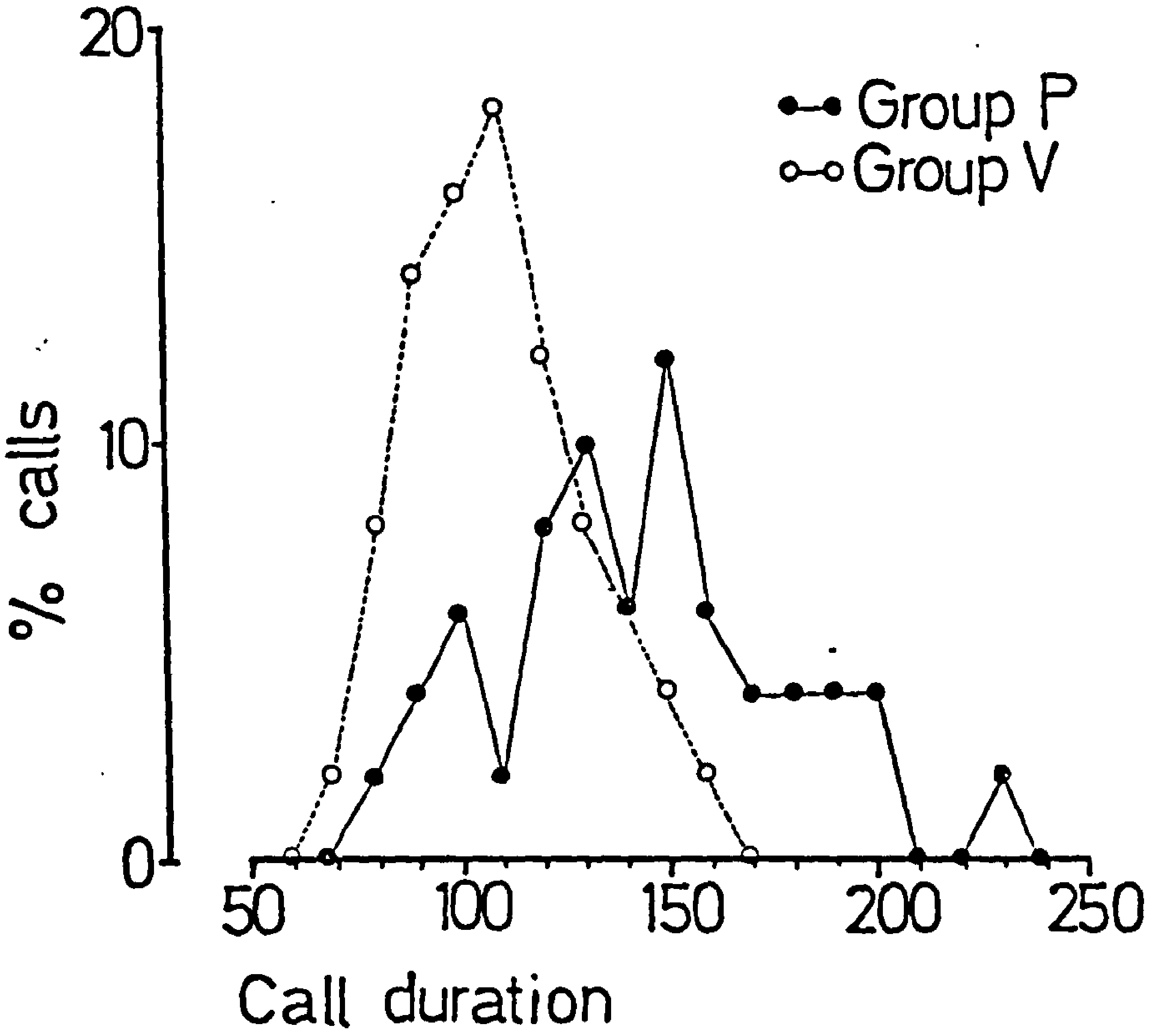
seconds to over 3 minutes. Group P called, over the year, each time for a mean duration of 141 seconds (n=107) whereas Group V called for a mean duration of 100 seconds (n=81). The distributions of call duration of the two study groups are quite different, with Group P calling for periods that were much more variable than Group V (Figure 9.17), as well as calling longer in each song.

The possibility that call duration related to group size was tested in each study area by comparing call durations from groups in which at least 3 voices were heard to those in which only 2 voices could be distinguished. The results (Table 9.9) proved that in every case the longer calls were emitted by the larger groups. Interpretation of this result rests on the assumption that Indri group size is directly related to the number of animals heard singing. Following the discussion of differences in the structure and patterning of the song amongst individuals in the two study groups (Section 3.4), this assumption appears to be justified.

The distributions of call durations in the studied populations were skewed, with relatively greater numbers of long than short calls. Once a group had begun to call it rarely stopped within 60 seconds, but could continue for much longer periods. It was not possible to determine external influences on changes in the duration of calls by the same groups on different days.

Mean call durations in the three study areas were

Figure 9.17 The duration of calls (in seconds) of each study group at Analamazoatra throughout the year.


20
10
0
% calls
50
100
150
200
250
Call duration
●–● Group P
○–○ Group V

STUDY AREA		<2 animals	>3 animals	t	p
VOHIDRAZANA	$\bar{x}$	79.1	120.7		
	n	59	47	6.49	<0.001
FIERENANA	$\bar{x}$	78.8	115.1		
	n	25	14	4.29	<0.001
ANALAMAZOATRA (excluding study groups)	$\bar{x}$	78.0	118.1		
	n	29	19	5.14	<0.001
STUDY GROUPS	$\bar{x}$	98.5	197.5		
	n	32	32	5.34	<0.001

TABLE 9.9. Group size and call durations.

	$\bar{x}$	n
VOHIDRAZANA	89.9	483
FIERENANA	80.0	188
(P) ANALAMAZOATRA	91.7	296
(V) ANALAMAZOATRA	99.6*	283

*includes most of Group P's especially long calls.

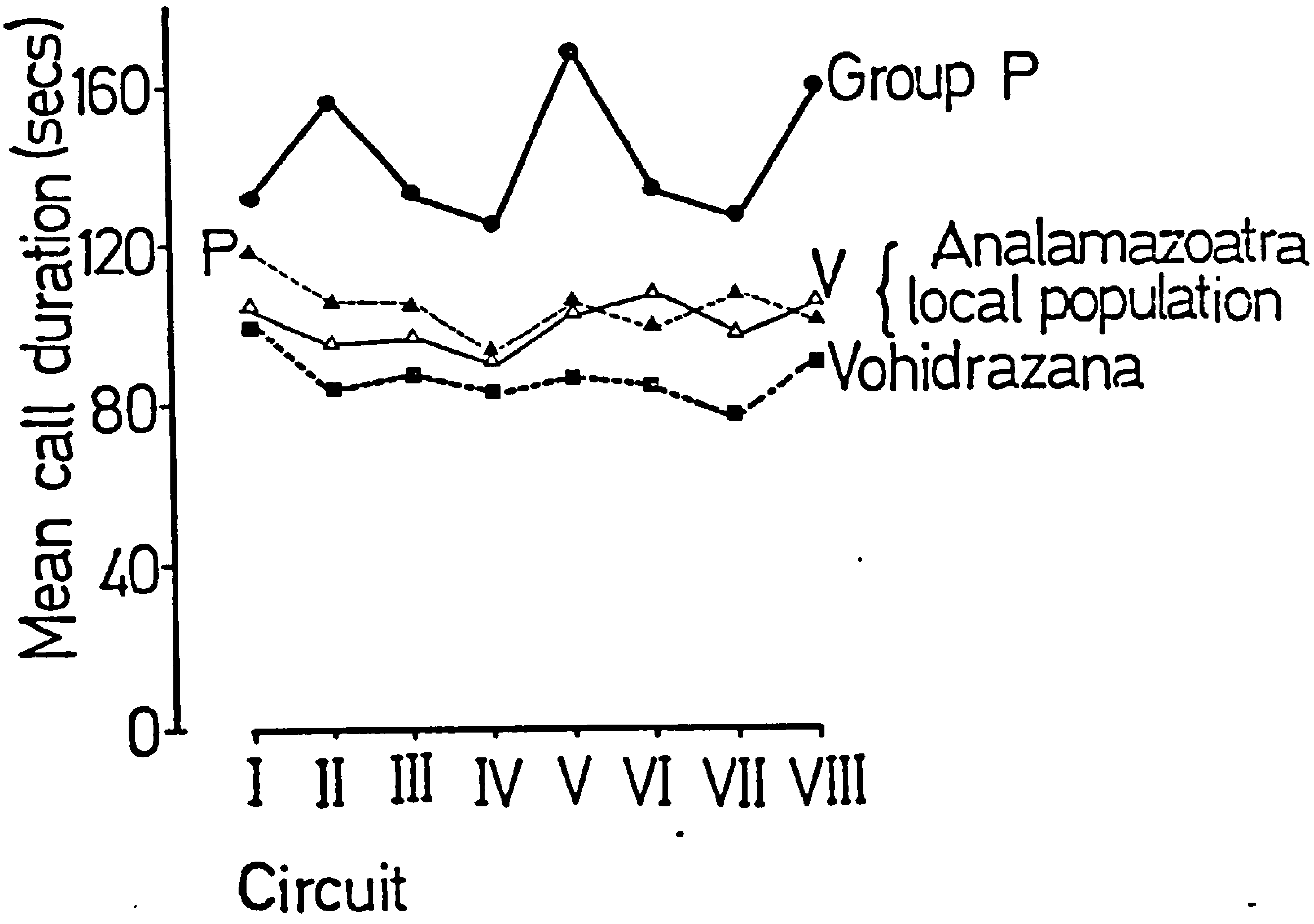
TABLE 9.10. Mean call durations in each study area.

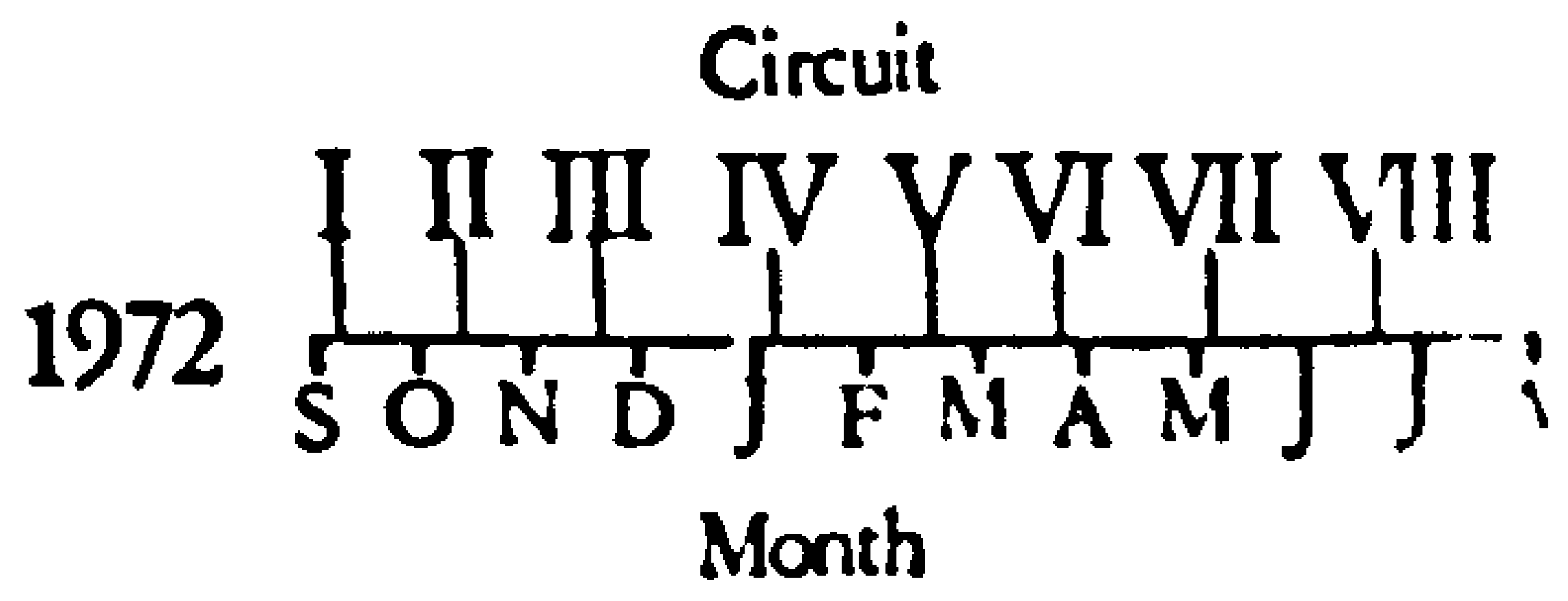
similar (Table 9.10). Due to the inclusion of the relatively very long calls of Group P in the sample from the population surrounding Group V, their longer mean call durations can not be meaningfully compared. The mean call duration at Fierenana was significantly lower than both at Vohidrazana ($t=4.04$: $p< 0.001$), and at Analamazoatra (Group P's local population) ($p<0.001$), but those of Vohidrazana and Analmazoatra did not differ ($0.6< p<0.7$). The significance of this variation is not completely understood, but may be due to the preponderance of small groups at Fierenana (see Chapter 4). The call durations of small groups in all study areas were similar to those at Fierenana, but the duration of calls by Group V (of identical group composition to all groups censused at Fierenana) were consistently longer.

The differences between Fierenana and other study areas in the duration of Indri song did not result from seasonal changes in call duration, as this did not vary consistently between areas or times of the year (Figure 9.18). The same differences were unlikely to have been due to different weather conditions as rain was seen to have no effect on Indri call duration (Dry v Very Wet: $t=0.14$, $0.8 < p < 0.9$).

In 53 (91%) of the 58 instances that Group P's calls occurred in clusters with other groups' calls, Group P calls were longer than 'cohesion' calls ($p<0.001$), the other 5 calls were judged to have been used for intra-group aggregation purposes. All normal calls from Group

Figure 9.18 Seasonal variation in mean call duration for Group P, the local population of each study group at Analamazoatra, and groups in the study area of Vohidrazana.


Mean call duration (secs)
160
120
80
40
0
Group P
P
V
Analamazoatra
local population
Vohidrazana
I
II
III
IV
V
VI
VII
VIII
Circuit


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
Month

P, therefore, were longer than other calls. The group's complement, 5 animals, was also superior to any other Indri group seen in any study area.

3.6 The Function of Indri Song.

3.6.1. Introduction

Loud calls have been interpreted by many authors as a mechanism of self-advertisement essential to some aspects of territorial defence (Marler 1965, Andrew 1972, Buettner-Janusch 1973, Tembrock 1974). Regular loud calls, which may be heard for over 1000 metres are emitted by titis, mangabeys, colobus, howlers, gibbons and siamang in addition to several lemur species, notably, Varecia variegata and Indri indri. As a rule these calls are emitted early in the morning or during the first hours of the animal's activity periods. Loud calls by primates may be instrumental in inducing members of different groups to confront each other at territorial borders (Ellefson 1968, 1974), may often evoke no recognisable change in behaviour, or may result in increased separation of groups (Chivers 1969, Waser 1975). In all cases a function of inter-group spacing has been attributed to the behaviour, and ecologists have been quick to point out that this may result in a more even pattern of environmental exploitation.

Careful distinctions have rarely been made, in discussing the 'territorial' function of loud primate

calls, between the following contingencies:

- (i) Representation of "self" so as to warn conspecifics of one's presence:
- (ii) Delineation of territory by border region definition
- (iii) Communication of 'possession' or occupation of an already defined territory. "Territory" is here assumed to be of permanent geographical situation over the considered period of time. It may be however, that a space around the group may be defended and comprise (for a ranging group of howler monkeys, for example) a dynamic territorial system (Chivers 1969)

Potential information mediated by loud calls may be classified into three divisions:

- (i) Information about the environment e.g. food, predators, weather.
- (ii) Information about the dispersion and distribution of individuals or groups e.g. location, distance or direction of individuals[1].
- (iii) Information pertaining to the characteristics of the calling animals e.g. age, sex, reproductive condition, group size and composition[1].

In the following discussion various possible functions of <u>Indri</u> song are tested from information obtained during the present study.

---

[1] This may include additional information about the activity of individuals or groups at a particular location.

3.6.2. Territoriality and Associated Functions

3.6.2.1. Influence of Calls on Ranging Behaviour

No relationship between the direction or distance moved by study groups following nearby calls was found (see Chapter 7).

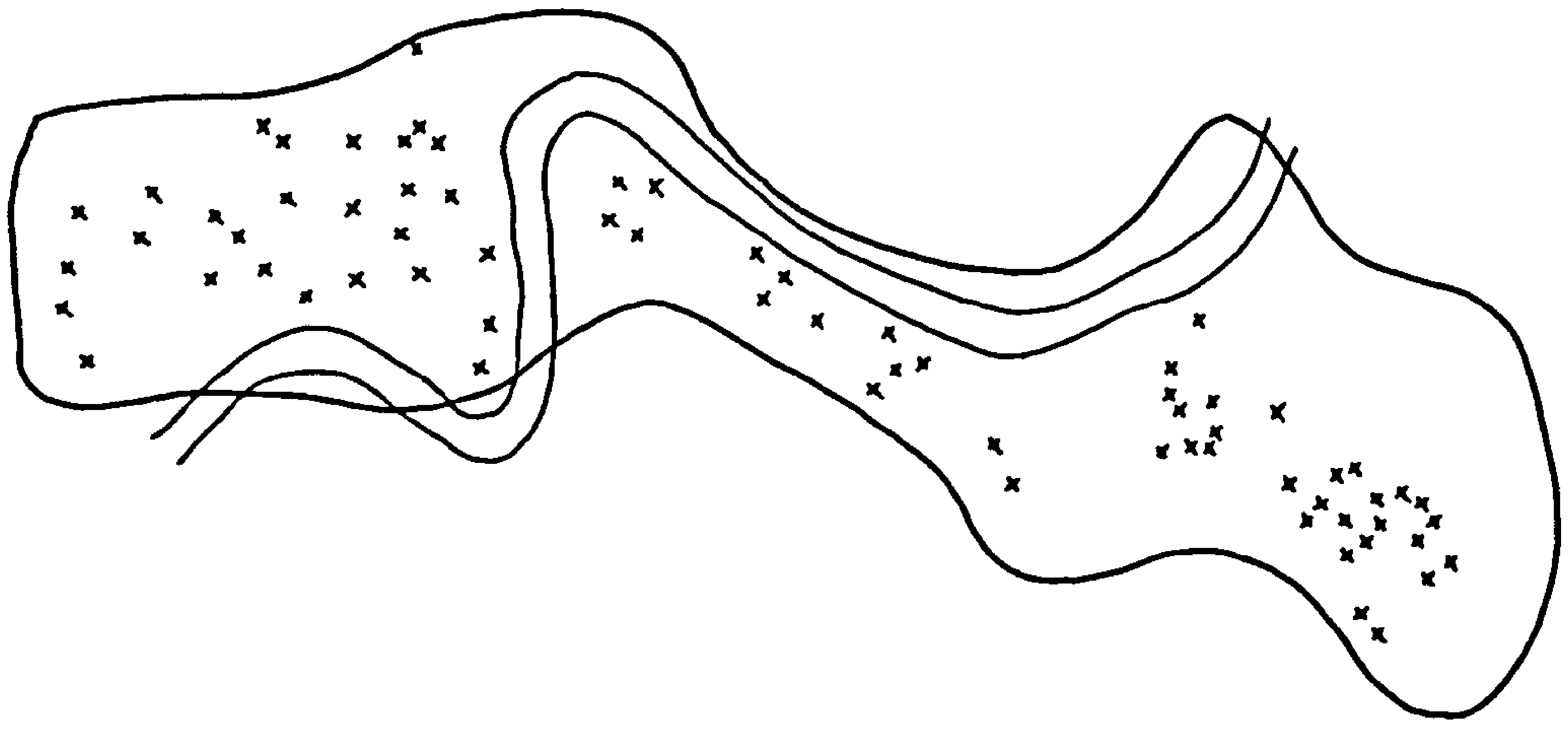
3.6.2.2 Territory Definition

Sound attenuating properties of the environment derive from many causes, and are complex and variable in their effects (see Appendix 5). As the distance of a sound source from a receiver may be innacurately communicated through highly attenuating media, the definition of a territory may not be precisely broadcast to distant groups. Calls from (i) peripheral locations or (ii) throughout the territory may, therefore transmit information primarily to groups living near the callers.

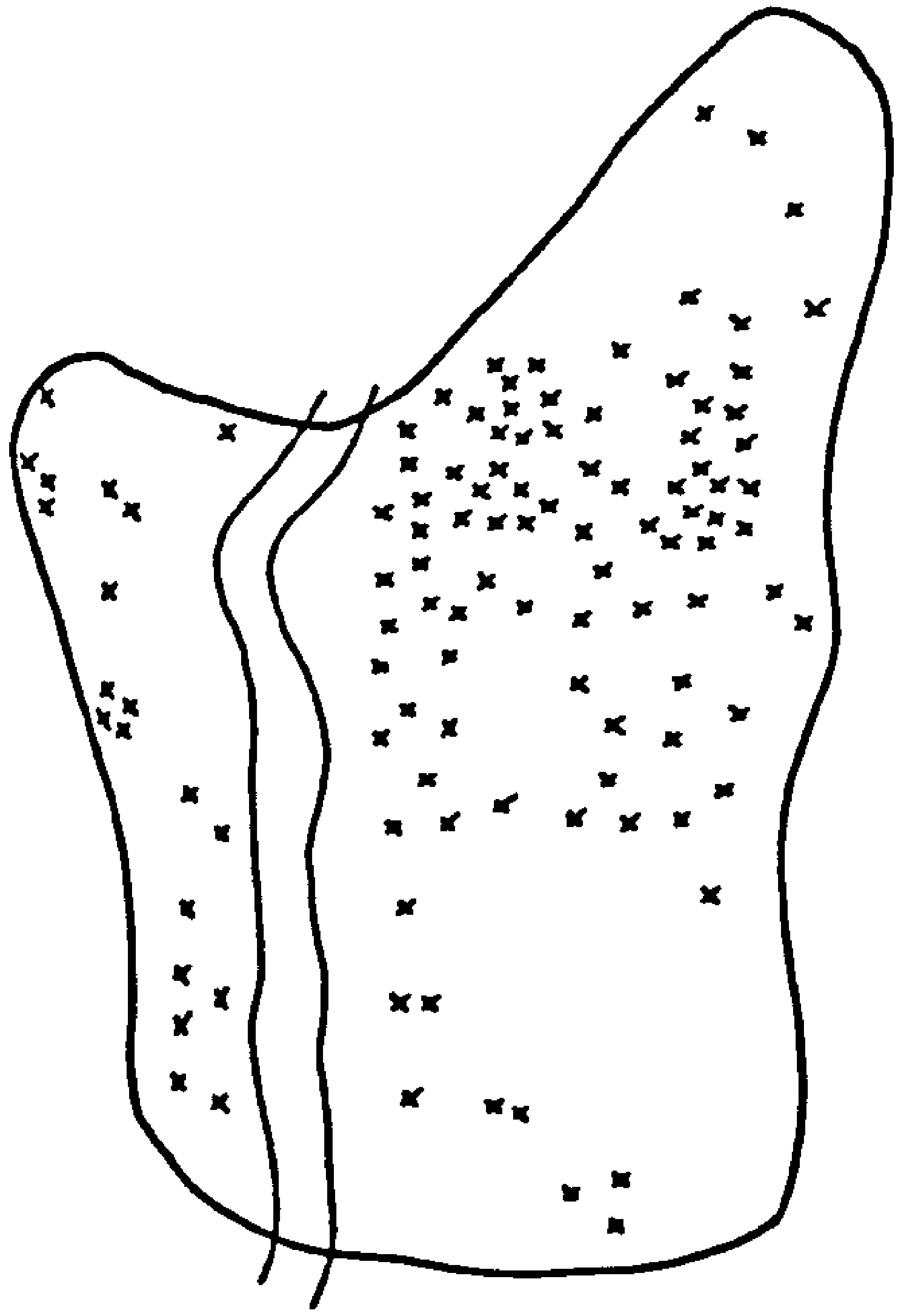
Indri in this study did not vocally demarcate peripheral locations (Figure 9.19). They called from any part of their territory, apparently in direct proportion to the amount of time they spent there. The relationship between quadrat use and singing location could not be statistically related, however, as there were too few calls in too many quadrats.

Over considerable periods of time an even song emission throughout all parts of a territory could define that territory to nearby groups, given that Indri could distinguish different groups from vocal idiosyncracies. There is no proof that this occurs, but there are

Figure 9.19 The location of spots where Group P and Group V sang in their home ranges throughout the year.



Group V



Group P

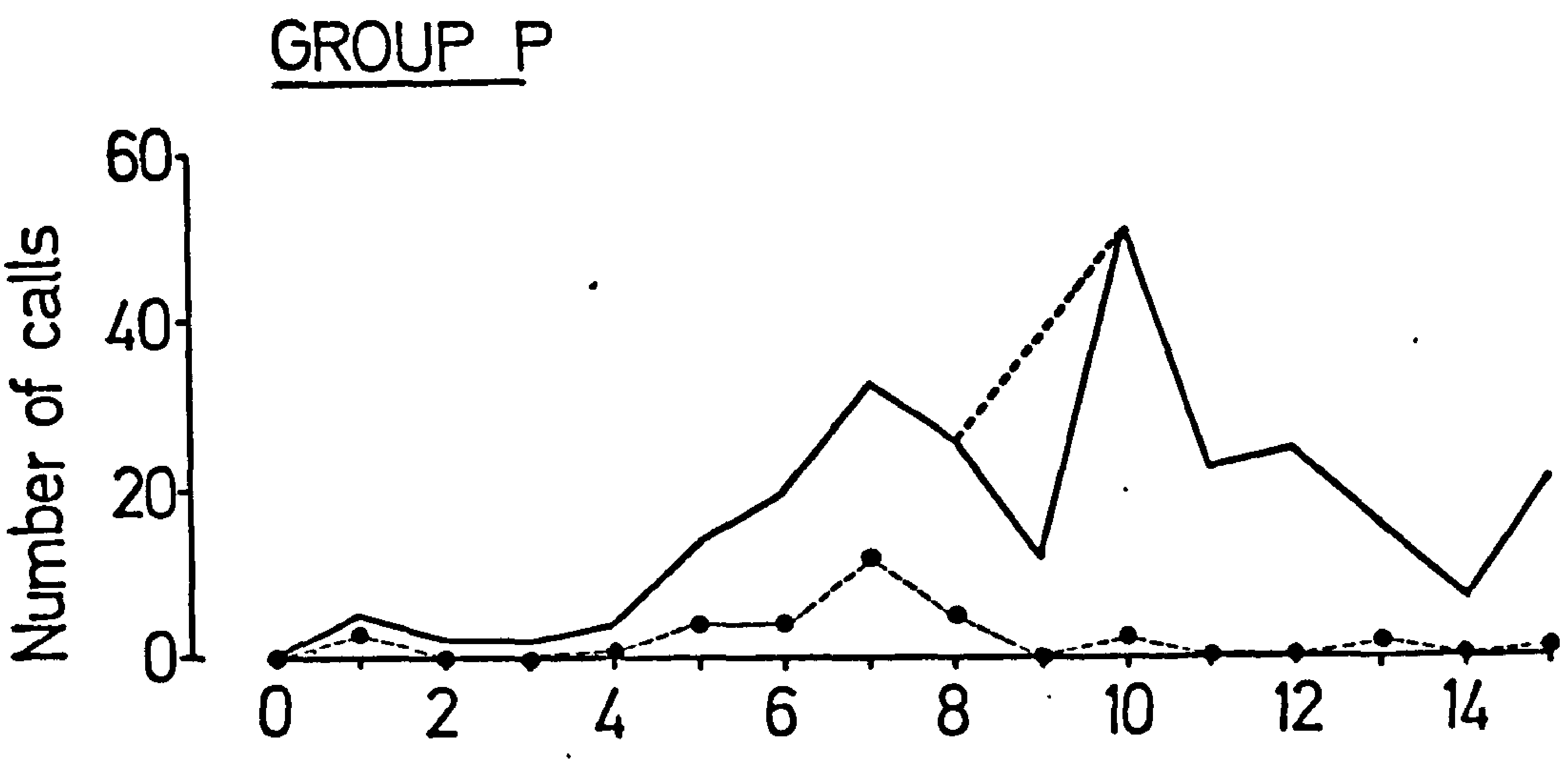
sufficient variations in song parameters (for example, those described in Section 3.4) to allow Indri song to differ substantially between groups. Alternatively, the declaration that a certain part of the environment is occupied, no matter by whom, may be sufficient for the receivers.

3.6.2.3. Territory Occupation

Vocal communication between neighbouring groups of Indri might be superfluous if visual contact was far more substantial than was apparent to a terrestrial observer. Furthermore, Indri groups rarely reacted to neighbours' calls (see below) and the call was therefore considered to be of greater significance to distant groups than to those nearby. Several calling signals could transmit information about gross measures of population density to a quite distant part of the forest. This feature may be facilitated by the tendency for both study groups to call following a call from groups situated nearby, although no other change in their behaviour was evident (Figure 9.20).

When the location of the calls replied to were actually plotted out it was apparent that Group V was responding mostly to calls from a specific region (Figure 9.21b), whilst Group P was not (Figure 9.21a). This was possibly due, however, to the distribution of surrounding Eucalyptus plantations (which did not support an Indri group) rather than reply specificity.

Figure 9.20 Differences between the distance of all calls in the population from the study group and those calls which the study group replied to. Data are shown for each study group throughout the year.


GROUP P

— Distance between group and all calls

●-● ○-○ Distance of calls group replied to

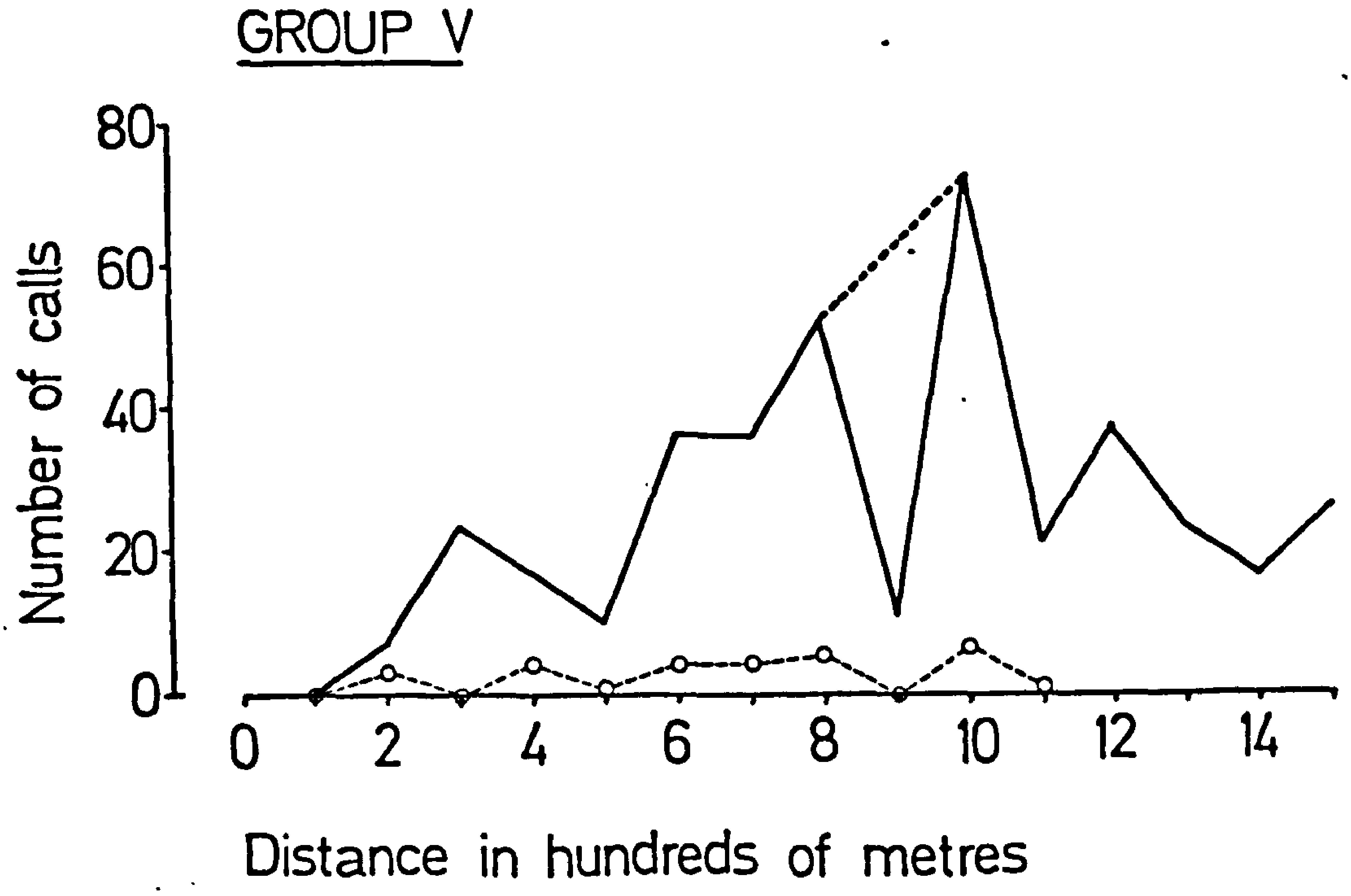
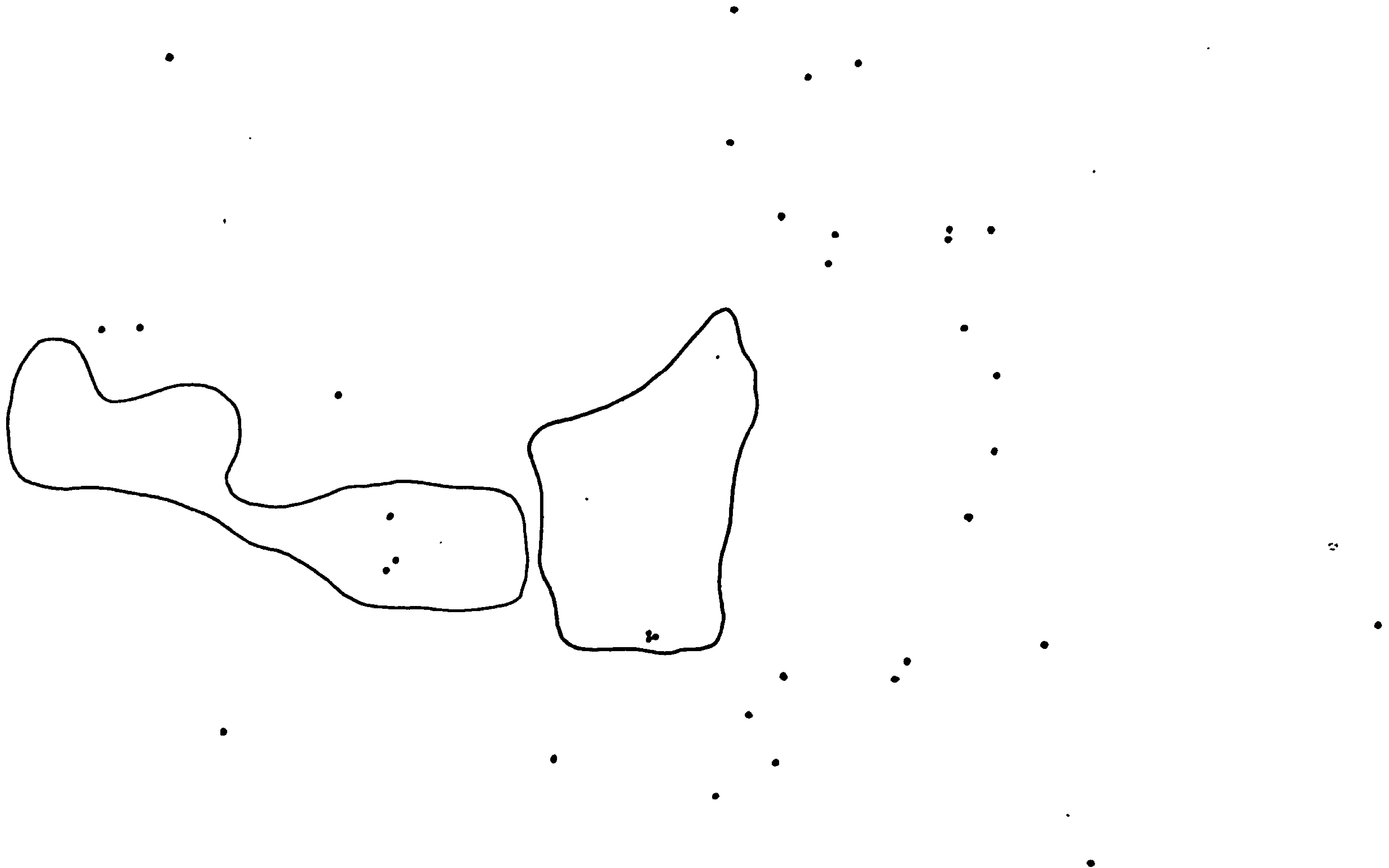
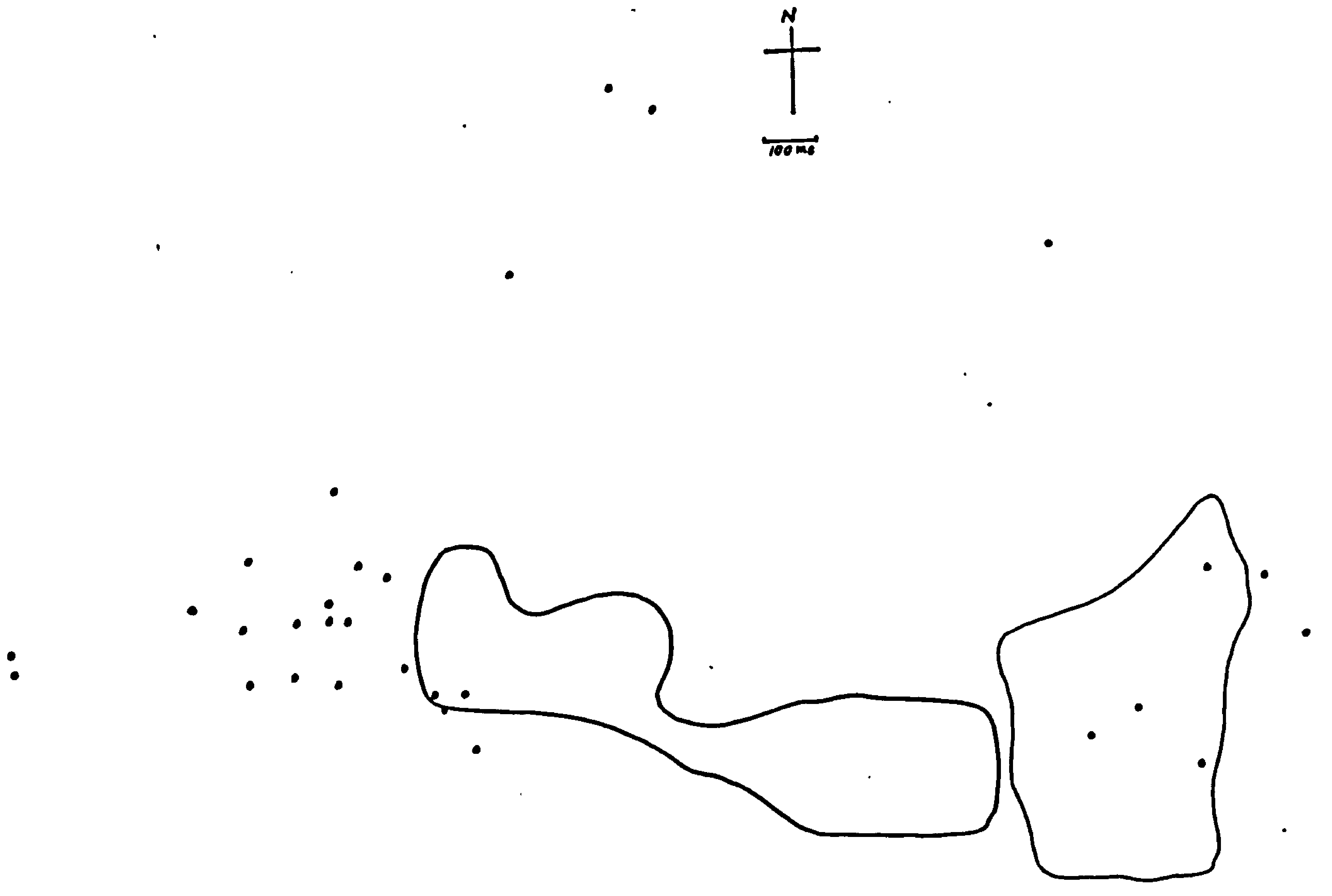

GROUP V

Figure 9.21a The location of calls replied to by Group P.



Group P

Figure 9.21b The location of calls replied to by Group V.



Group V

3.6.2.4. Territorial Defence

When two _Indri_ groups approach each other at a common territorial border intense displays of movement and calling take place. Although only 8 border encounters were fully observed during the course of the study, these appeared to be of two main types:

(i) Border encounters developing from the 'chance' proximity of two groups ranging at the same time in the same area (4 cases observed).

(ii) Border encounters issuing from perception by a group in a central location of a neighbouring group (either visually or by auditory clues) in, or even just _inside_, the group's territorial border (4 cases observed).

Indri territories partition the forest to a large extent into group-exclusive portions. Surrounding each territory is a narrow band (in the 3 cases where this was measured its width varied from 30 - 50 metres) of common land in which only 2 groups ranged (Figure 9.22). This common land was normally used for ranging and feeding activities by each group in their daily activities the group _always_ turning, on reaching its outer limit to travel towards the centre or along the edge of the home range. On 4 occasions 2 _Indri_ groups were seen to meet, following apparently normal ranging patterns, in this area. No strange or anticipatory behaviour was seen in the period preceding the encounter. In Group P such an event occurred on the 22nd of November 1972:

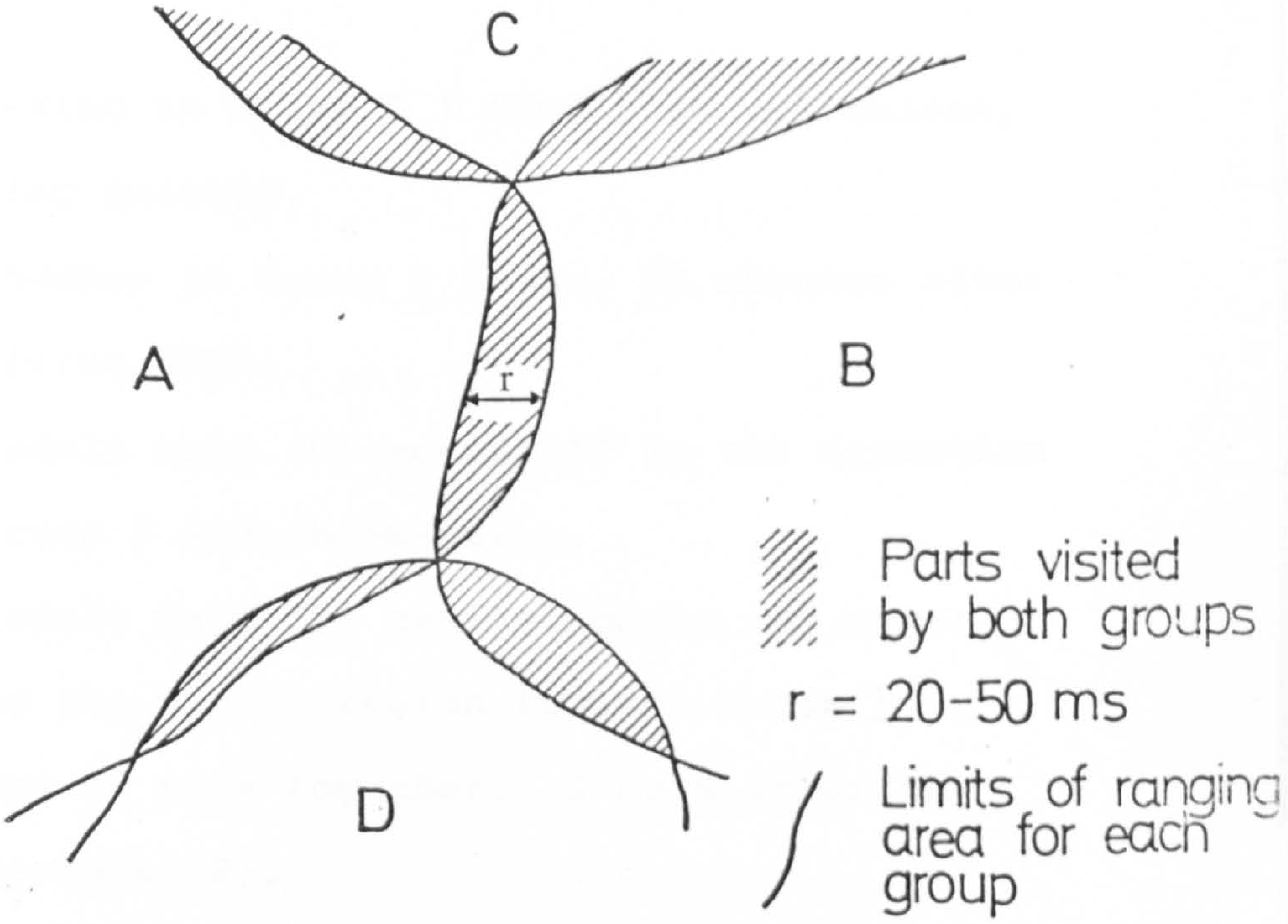
" ......0835 Single HOOT[1] by an individual from the

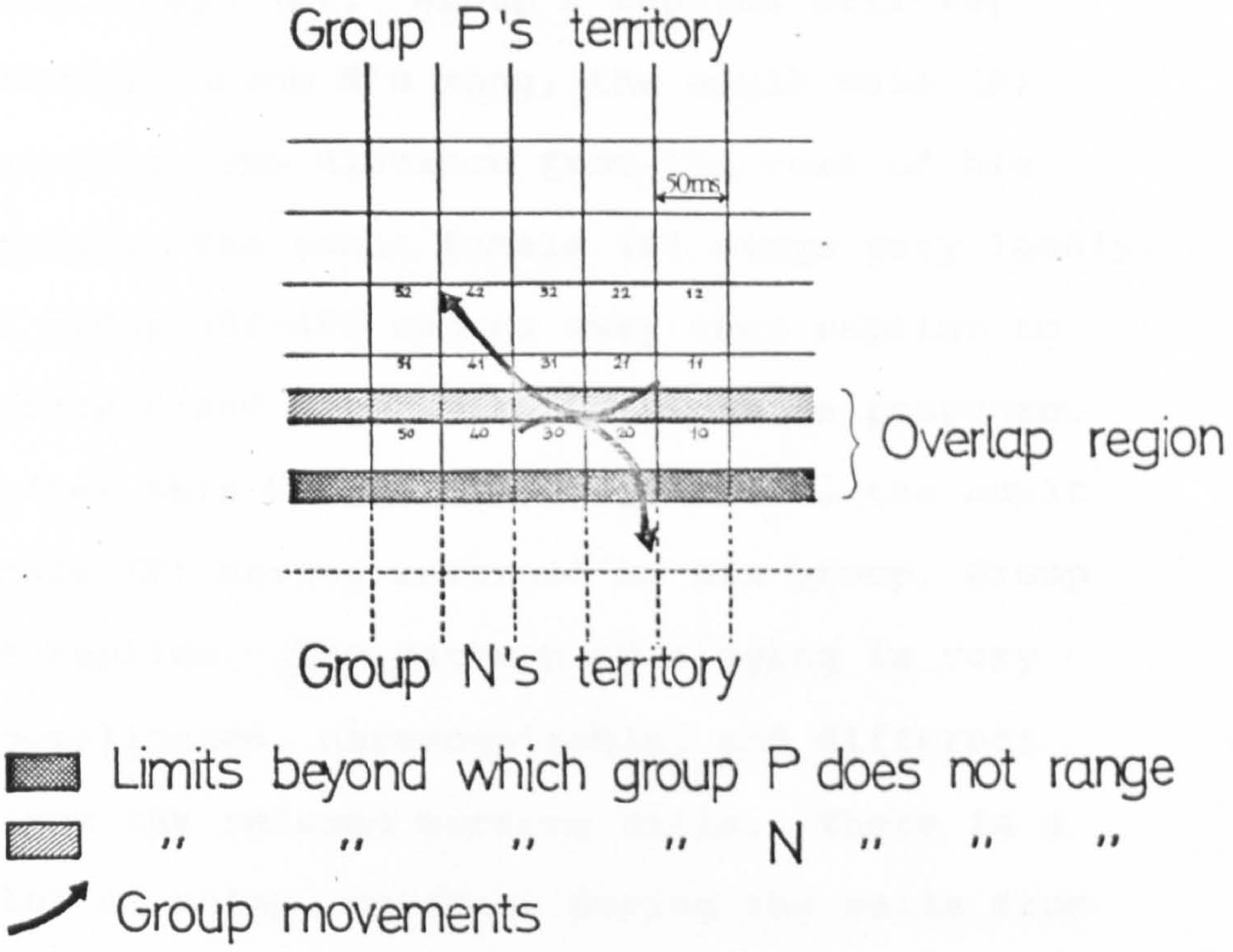
---

[1] Ground predator alarm call (Appendix 6), here evoked by the observer's presence.

Figure 9.22 Diagrammatic representation of border regions between neighbouring *Indri* groups.

Figure 9.23 Movements of Group P and Group N during a border encounter.


C
A
B
D
r
Parts visited by both groups
r = 20-50 ms
Limits of ranging area for each group


Group P's territory
50ms
52
42
32
22
12
51
41
31
21
11
50
40
30
20
10
Overlap region
Group N's territory
Limits beyond which group P does not range
" " " " N " " "
Group movements

neighbouring group (N) - which had been mistakenly identified as 03 from Group P - in the border region, 150 metres from Group P.

0845 Returning to Group P I find them motionless, resting quietly.

0911 One member of Group P jumps, 28 minutes after the first HOOT.

0918 The adult male (P) moves off in the direction of Group N and cheek-marks.

0924 The adult male (P) genital-marks and moves along the border region towards Group N.

0926 03 and 02 play together. I move after the adult male (P).

0928 Both groups suddenly roar simultaneously and Group N sings, 20 to 30 metres away from the adult male (P). Group P replies half-way through Group N's song, the adult male (P) singing some distance from the rest of his group. The adult female (P) sings very loudly. A group 300-400 metres away then replies to Group P and Group P again sings in response. After this Group N sing again and, the adult male (P) having returned to his group, Group P replies. The pattern of singing is very complicated, unrecognisable, and different from the relaxed morning calls. There is a lot of animal movement during the calls from both groups. The adult male (P) defaecates whilst singing.

Group N then replies to Group P and this is followed by a call from Group V, 6-700 metres away.

0942 The calls end after a distant group calls about 1000 metres away to the north-east. Group P had been singing continuously for approximately 9 minutes.

0955 After more calls from Group N and Group P the former moves from quadrat 30 to the quadrat (unmarked) south of 20 (Figure 9.23). Group P moves from quadrat 21 - 31 ......"

Later on the same day Group P suddenly moved 300 metres northwards to the other end of their territory, but this occasionally happened anyway during the normal ranging activities of the group.

Similar patterns of singing and movements were observed in Group V, Group IV and in an unhabituated group at Analamazoatra. During all these encounters the adult males of each group appeared to be the animals nearest to each other. It is not impossible that physical combat occurred - the Group P adult male had most of one ear missing and one adult male (Group U) had lost his right eye.

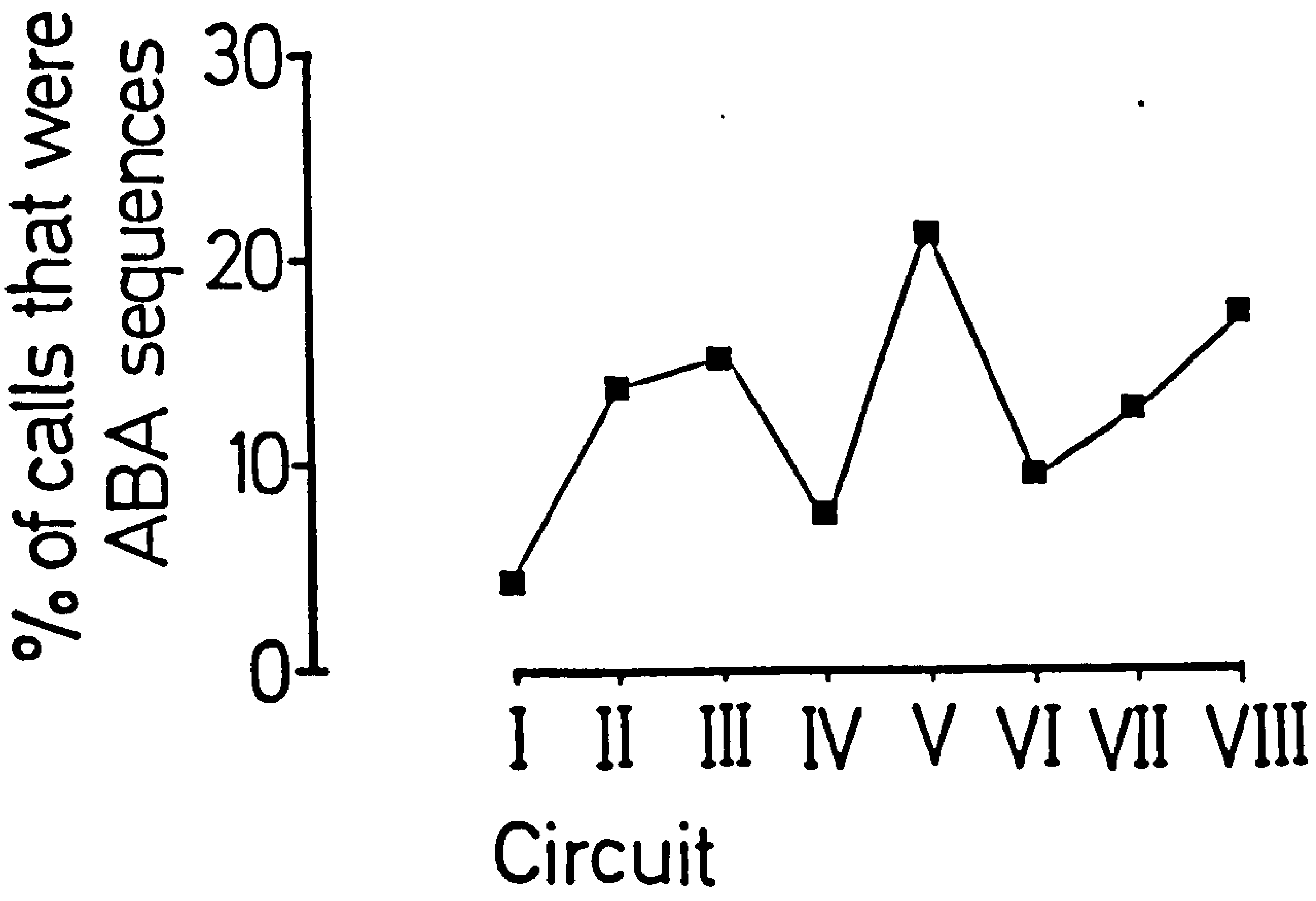
Type (ii) encounters were probably more common than Type (i) encounters. Frequently the observer, during census walks, came across unhabituated Indri in strange group configurations: groups of 2 or 3 animals separated by some distance from one other animal. Retrospective analysis of the singing patterns indicated the presence of two rather than one group of Indri in these locations. On the 6th March 1973 the significance of this configuration was understood from observations on Group V: A neighbouring group sang from well inside the border region. Group V clearly recognised this group's invading position, despite their location 250 metres away. The adult male of Group V immediately left the adult female with infant, after they had replied, and rushed off to the border region. Once there he started to sing and was accompanied as usual by the adult female despite their separation. After this, there followed a succession of alternate calls from the two groups, the invading group farther and farther away on each occasion. After an additional 30 minutes the adult male returned to the female and normal ranging and feeding activities resumed. There were many calls in the population where a singing pair of Indri appeared to be widely separated and it is probable that on these occasions the adult male was confronting a neighbouring group.

Territorial defence in the two ways described above was rarely witnessed and may have been extreme examples of more common forms of interaction between specific groups. A very common feature, for example, was a simple vocal interaction between two groups, usually 200 to 400 metres apart, in the singing pattern "A-B-A", the group calling first also ending the interaction. When groups were very close the repetitions could be continued and prolonged: ABAB or ABABA etc., grading continuously into the patterns described above, where physical confrontation is also present.

There was no evidence from observations on the study groups that seasonal increases in calling behaviour resulted from a greater incidence of these types of calling sequences, but a further examination of a whole population (Vohidrazana) was made in order to confirm this. It was considered possible that if seasonal changes in the tendency to range near border regions occurred, inter-group relations could be easier understood. A mean of 12.2% of the calls at Vohidrazana were found to be of "ABA" format, and 12.4% of the calls recorded at Fierenana also occurred in this pattern. The percentage of these calls did not increase at any particular time of the year (Figure 9.24). It appeared that these types of calls may have occurred more often early than late in the morning (Figure 9.25), although at Vohidrazana this difference proved to be non significant ($X^2_{1df} = 3.194 : 0.05 < p < 0.1$).

Another property of the population's calling behaviour was the apparent unequal geographical distribution of calling activity at Vohidrazana - the only study area where such positional heterogeneity could be exposed thanks to the large numbers (about 40) of groups that could be heard from one position. In order to examine the presence of "hot spots' in the population, which could not be attributable to only one or two vocal exchanges, the proportion of calls deriving from different sectors of the forest were compared. Only

Figure 9.24 Seasonal variation in the proportion of calls classified as ABA sequences at Vohidrazana.


% of calls that were ABA sequences
30
20
10
0
I
II
III
IV
V
VI
VII
VIII
Circuit

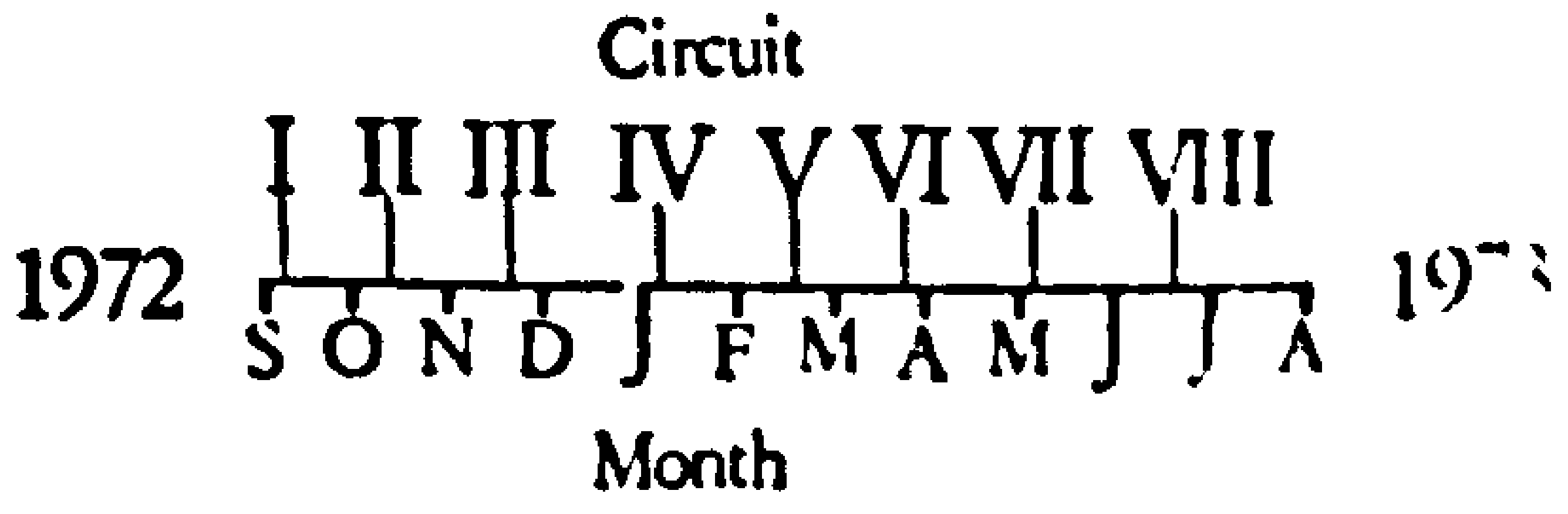
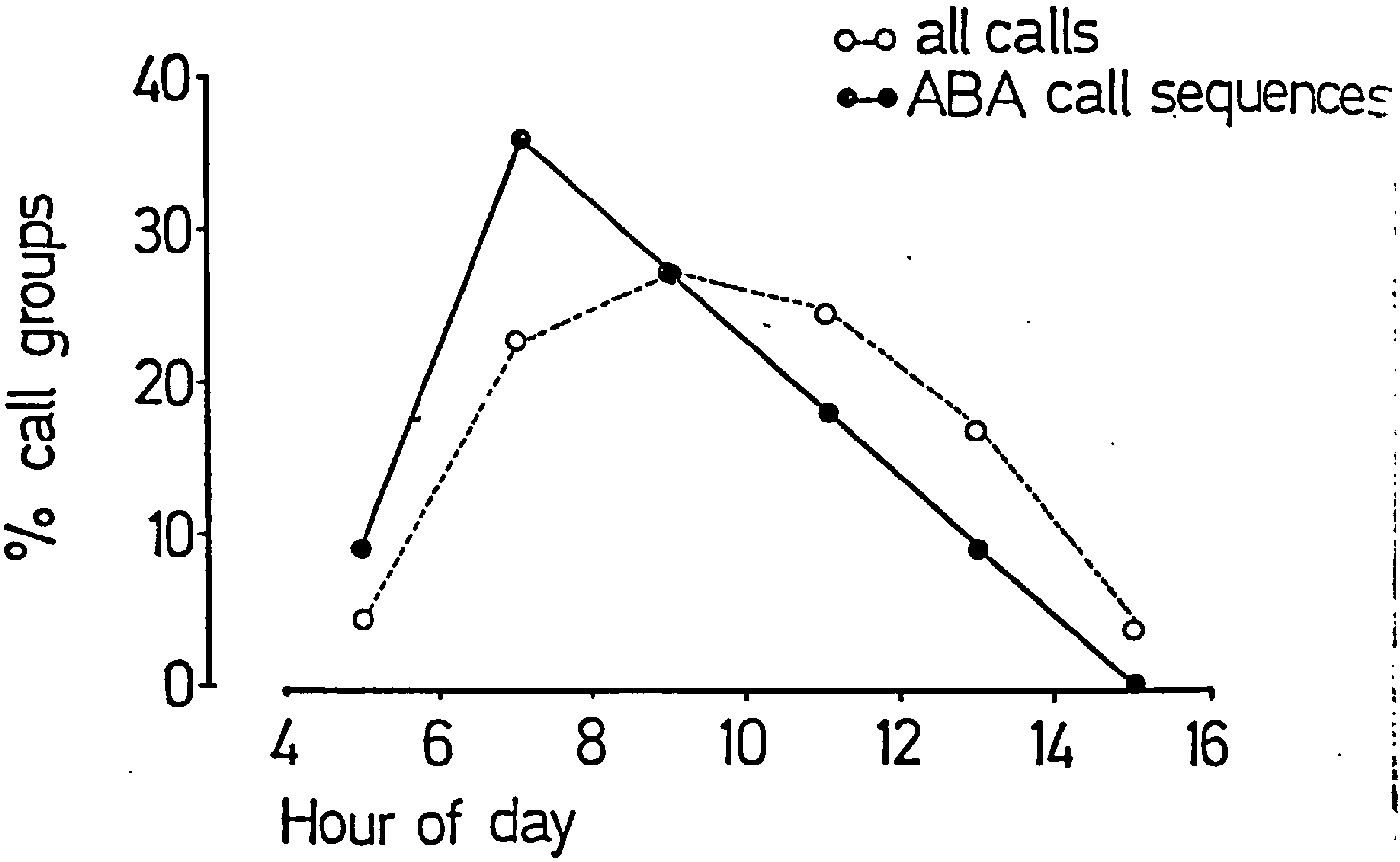
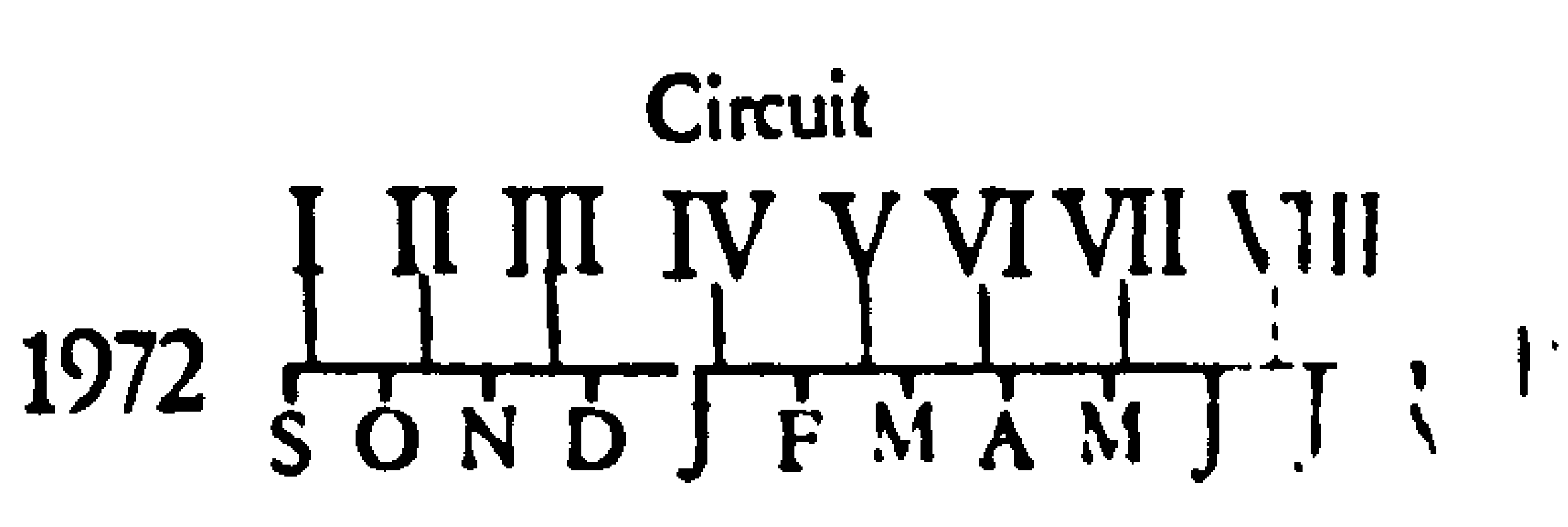

Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
Month

Figure 9.25 Hourly distribution of calls classified as ABA sequences at Vohidrazana throughout the year.


o-o all calls
●-● ABA call sequences
% call groups
40
30
20
10
0
4
6
8
10
12
14
16
Hour of day


Circuit
I II III IV V VI VII VIII
1972
S O N D J F M A M J
Month

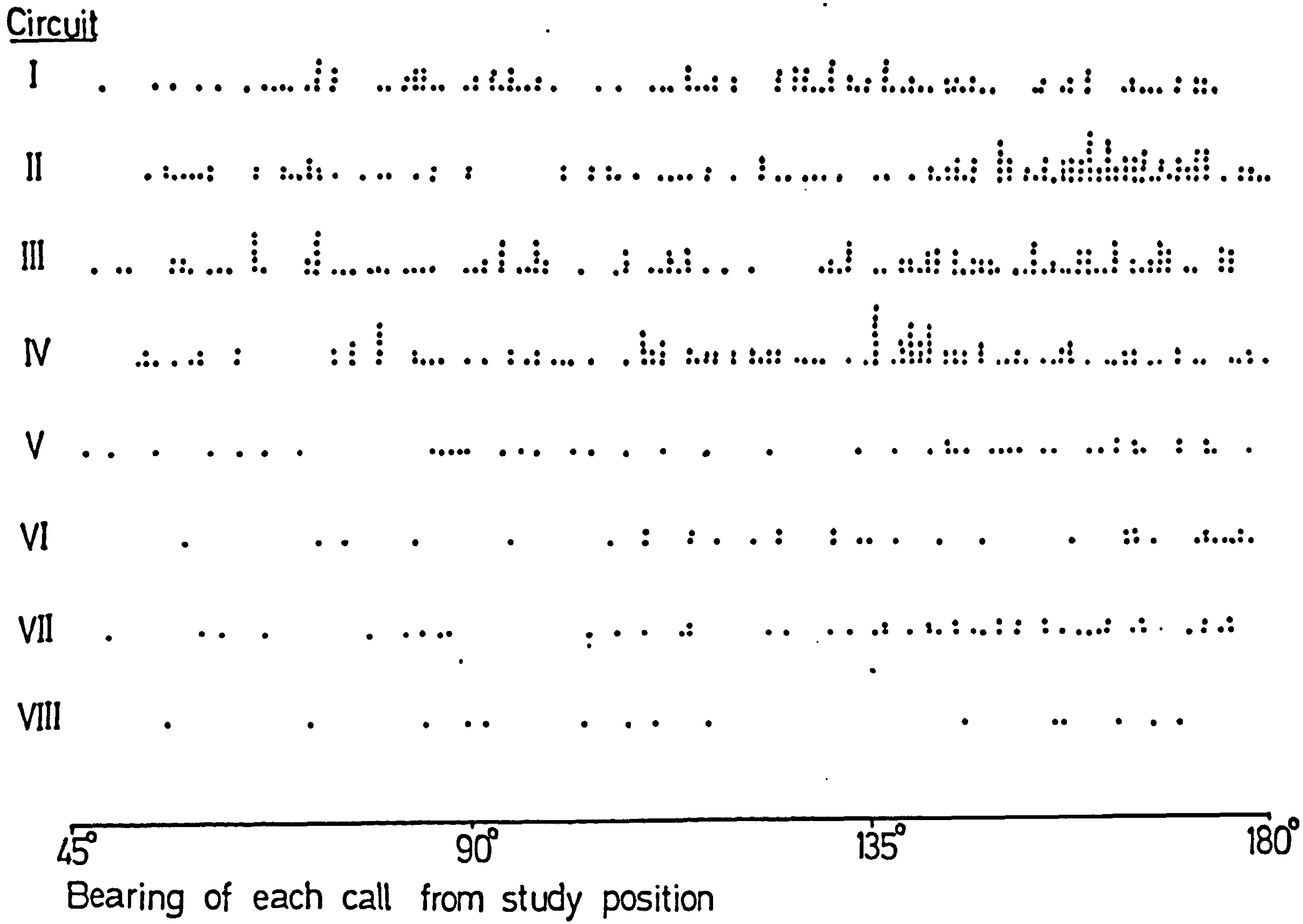
those parts of the forest which could be directly viewed (and were thus attenuating sound by only a single canopy layer) were considered (Figure 9.26). Gross differences between the northern and southern sectors were compared by a Sign Test and found to be significantly different ($p < 0.001$). Each segment of 10° was then examined by a Friedmann One way Analysis of Variance and found to be significantly variable ($X^2(r)_{(12df)} = 35.93$: $p < 0.001$). It was not possible to determine whether these areas of high calling activity contained calls of a specific format, pattern, or duration: but there was no preponderance of distinct calls. It is possible that Indri territories vary somewhat in size and groups living in areas of high population density may require different (more frequent) calling behaviour for territorial defence, than others.

The role of Indri song in territorial behaviour appears to be complex. In all probability calls were not an influential parameter in normal ranging behaviour, but when groups came near to each other, they could induce movement and confrontation. As well as performing a central role in inter-group encounters, they were also emitted in relaxed morning exchanges with groups up to 1100 - 1200 metres (or more) away, on 2 out of every 3 days.

3.6.3 Group Cohesion

Occasionally members of Group P would become dispersed - the group dividing into aggregations of 3 and 2 individuals - or into even smaller denominations. If this

Figure 9.26 The location of high- and low-calling regions in a forest populated by *Indri* (Vohidrazana). Each point represents a call heard from a certain direction within 1000 metres of a constant position taken by the observer. The relatively frequent calls from a sector 130°-180° are emitted throughout the year.


Circuit
I
II
III
IV
V
VI
VII
VIII
45°
90°
135°
180°
Bearing of each call from study position

dispersion resulted in independent ranging of individuals or pairs separated by over 100 metres, Indri might sing in order to effect reaggregation. The song, identical in structure and volume to morning calls, differed from them in four ways:

(i) it could be initiated by any individual

(ii) it was performed at a slower tempo and for a shorter duration:

(iii) it contained silent intervals that might last for several seconds:

(iv) it possessed no consistent pattern, any individual singing at any time. Usually only one animal sang at a time.

The call was judged to be cohesive in function when these characteristics and the relevent context of group dispersion was present and subsequent aggregation of animals occurred. During the re-aggregation of the group, some animals remained stationary and the others moved towards them. How it was established which animals should move and which should wait remains undetermined. On one occasion, however, all individuals moved and met at a dense food source.

Cohesion calls often but not always contained a 'roared' introduction as did most other calls. Sometimes the roar sufficed for contact to be re-established and in these cases the song was dispensed with or was very short.

Twenty three of the 114 calls emitted by Group P (20.2%) were judged to have been 'cohesion' calls and these were mostly confined to Circuit lV (see Chapter 8). During the other Circuits only 7% were considered to have been made for cohesion purposes whilst during Circuit IV 61% when the adult female was wounded, were so judged.

3.6.4. Non Territorial Aspects of Inter-group Communication in Indri

Indri song appeared sometimes to be induced by potential 'predators' e.g. birds of prey, aeroplanes, thunder, the observer (for unhabituated groups), and could therefore have conveyed information about such events to conspecifics and, maybe, other species. No difference was apparent in the structure of these calls from normal vocalisations.

In addition the patterning of the calls of Group P - the asynchrony of the adult male and 03 in singing with the adult female - was so disciplined as to suggest it to be a characteristic of all Indri groups the size of Group P, and possibly for it to have been of communicative importance. It is possible that from other varying properties of this group's calls i.e. call duration and young animals' differing participation, information about group composition and constituents' age and sex may have been transmitted to other groups.

Monitoring other groups' complements may be of great importance in pair-bond formation for slowly maturing, family-living animals with birth seasons at long intervals. If mate location is a problem for

Indri the approximate position of an individual of the correct sex and of the right age may be advertised by this means, and by scanning large numbers of groups over some time this may inform a maturing offspring that potential mates are available in certain areas, obviating the need for close perhaps dangerous physical contact with many groups.

The process by which new Indri groups are formed remains conjectural. The possible role of individuals (probably males) who range across other territories has been already discussed (Chapter 7). It may be, however, that excessive genetic homozygosity can only be avoided if newly adult animals range considerable distances to locate mates. In these cases the ability to sense regions containing suitable individuals may maintain a high premium.

4. DISCUSSION

Indri song, it has been suggested, should be most profitably considered to have several functions. This conclusion is recognised to have arisen in part from an inability to prove a definite single function, and will, therefore, be modified in future studies.

Indri song may play a part in active territorial defence, proclamation of a territory, definition of that territory, group cohesion, communication of environmental conditions and the reproductive potential of individuals. It is of heuristic value to construct an integrated model of the inter-group communicative behaviour exhibited by Indri. The model (below) can not however, be supported by conclusive evidence at the present time :

(i) Indri call to state (a) occupation of an approximate region in the forest, to distant groups or individuals, (b) present location within an already defined area (defined possibly by repeated group confrontations), to neighbouring groups.

(ii) For animals which may be nomadic, calls from parts of the forest over a period of time indicate to an approximation the population density within that region (and hence the potential for territory formation). The actual regions occupied may be communicated to these individuals by scent-marks in the territory, as envisaged in Section 2.7 . Characteristics of some groups' calls may provide information on the reproductive state of their constituents. Both these features may have significance only at certain times of the year.

(iii) A single call is purported to transmit, therefore, different information to different individuals or groups. As suggested above, the actual lines demarcating a territorial boundary may be established over a long period of time - probably several years - by group confrontations that are lengthy, intense and perhaps traumatic for the individuals involved. This is important for it probably facilitates memory of the exact location for both groups. The completeness of the propriety in this case, would vary with time.

(iv) Neighbouring groups therefore, probably know each other rather well. The most likely role of scent-marking (if this is indeed communication directed outside the group lies in its signalling properties for conspecifics who have abandoned or lost strict ranging limitations and are, therefore, not involved in inter-group encounters.

5. SUMMARY

1. Scent-marking actions are performed by adult, mostly male _Indri_ either spontaneously or when disturbed by conspecifics, predators or other animals. No specific regions of the territory were marked more than others, but often the same spot on one tree would be re-marked on subsequent visits.

2. _Indri_ groups regularly emit loud morning calls in a wailing "song" that may last up to 4 minutes. The calls are given in response to neighbouring groups' calls, disturbances, when group members become dispersed and during border encounters. The calls may be heard by other _Indri_ groups up to 3000 metres away. Several parameters of the song vary according to group size and group composition in terms of the age and sex of the constituents, and, perhaps their reproductive state. Calls vary in frequency according to season (more calls occurring prior to the mating season than after it) and to the prevailing atmospheric conditions.

3. The function of scent-marking and loud calls may vary according to the identity of the conspecifics receiving the information. Thus for nearby or adjacent groups calls are part of territorial defence displays and may advertise accurate information about the position of groups within their territories. For distant groups the information transmitted may concern measures of population density in large areas or the reproductive

state of individuals. Indri ranging without territories may be warned of the presence of conspecifics by scent-marks.

CHAPTER 10

Infant Development

1. BEHAVIOUR OF THE NEW-BORN INFANT

New-born Indri are first visible as a tiny, black form clinging transversely to the lower part of the mother's abdomen. An infant at this stage was first observed on the 26th May 1973 in Group IV at Vohidrazana. It appeared to be very young, perhaps only a few days old, although as this group had not been observed since the 23rd April it could only be certain that the infant was less than 4 weeks of age[1].

The infant's eyes at this time appeared to be permanently closed and it burrowed deep in the mother's abdominal fur. The only activity of the infant was infrequent attempts to crawl up the side of the body to the nipples with the mother occasionally raising the appropriate arm to allow better access (Plate 10.1). The infant was not otherwise placed at, or directed to, the nipple by the mother any time.

The Group V infant was first seen on 18th July 1972 (the first day this group was observed) in an obviously more advanced state. All 13 infant Indri seen during the course of the study were at physically corresponding stages at the same time and this provides the only concrete evidence that Indri reproduce seasonally,as do all other lemurs for which there is information (Petter 1962, Petter-Rousseaux 1964)

The first unrestricted observations of the new-born

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[1] The 15th May - the date midway between these two dates when the infant was born - is henceforth regarded as the birth date for Indri for easy reference. The spread of births over time in Indri is unknown, but from size comparisons of observed infants is probably less than one month.

PLATE 10.1 The adult female of Group IV (Vohidrazana) in 'arm-raised' posture allowing infant (approx. one month of age) access to axillary nipple.

PLATE 10.2 'Play-pen', resting position of adult female of Group IV (Vohidrazana) allowing infant (approx. one month of age) security and movement about her lower body.

infant in Group IV were made on 28th May 1973. Little hair covered the thin, lanky body and the face was entirely hairless. The infant was quite active, nosing and burrowing into the mother's fur, placing it's head over the mother's arm, and moving around the abdominal region.The mother's areolar area was prominent, the nipples large and projecting.

On the 30th May the infant was seen crawling over the mother's chest and neck. It was frequently licked by the mother as various body parts became exposed. In resting or sleeping psotions the mother stretched out her legs, her arms holding the horizontal branch supporting her weight, thus forming a playpen-like structure inside which the infant moved about safely (Plate 10.2). The sleeping female folded her body over the infant in this position, thereby totally enclosing it.

Changes in the pattern of grey and black hair were observed on 10th June 1973, when the infant was next observed. The infant, now about 3 weeks old, actively crawled all over the mother's body and large male genitalia were clearly visible at this time. The infant's activity was restricted mostly to the afternoon and appeared to coincide with a reduction of feeding by the mother. At this stage the infant was first observed clenching, unclenching and biting its own hand.

The mother took little positive interest in the infant during these first 2 - 3 weeks. She was not seen to restrict its movements or otherwise appear to influence its activity. No other group members approached the adult female or took any interest whatsoever in the infant.

2. SUCKLING BEHAVIOUR

Suckling was observed until the Group V infant was at least 1 year old, but feeding on the vegetation from 30 weeks of age was associated with a reduction of observed suckling activities. From the age of 10-12 weeks the suckling position of the infant was from behind[1] in the carriage or sleeping position (Plate 10.3), and it was often difficult to determine whether the infant was resting or suckling.

The timing of suckling bouts and their effect on the activity period has been discussed in Chapter 3. The number of suckling bouts, the number of days on which suckling occurred and the total time spent suckling increased together to peak during the mid-summer period when the infant was 30-35 weeks old (Figure 10.1). Suckling by the Group V infant during Circuit I was probably infrequent but in any case the activity was too discrete to distinguish with certainty when the female rested with the infant immobile on her chest.

Daily variation in suckling behaviour was great. Bad weather altered the timing rather than duration of suckling - on wet days suckling being delayed until the short activity period had ended. During each day of Circuit III between 1 and 8 bouts of suckling occurred,

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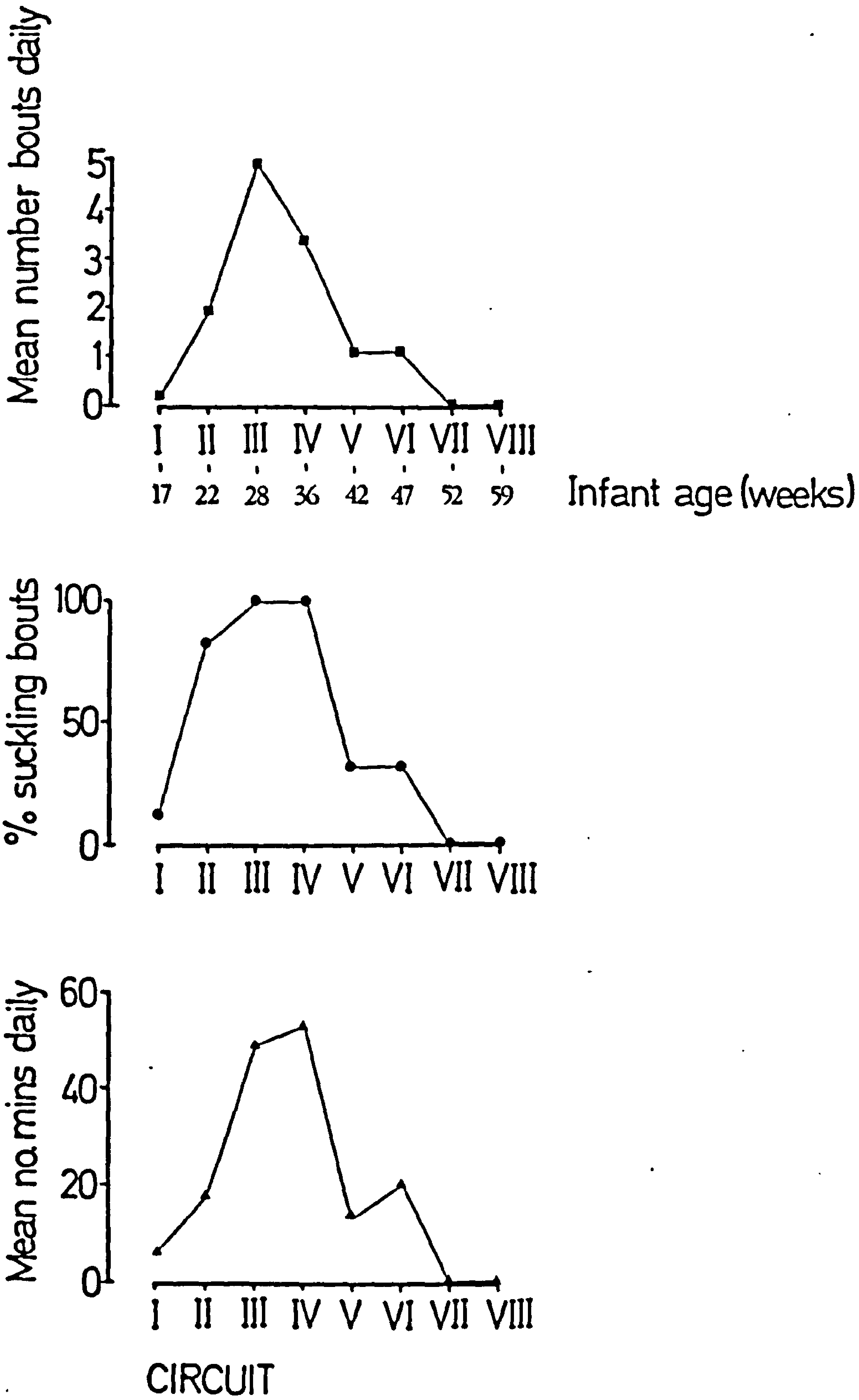
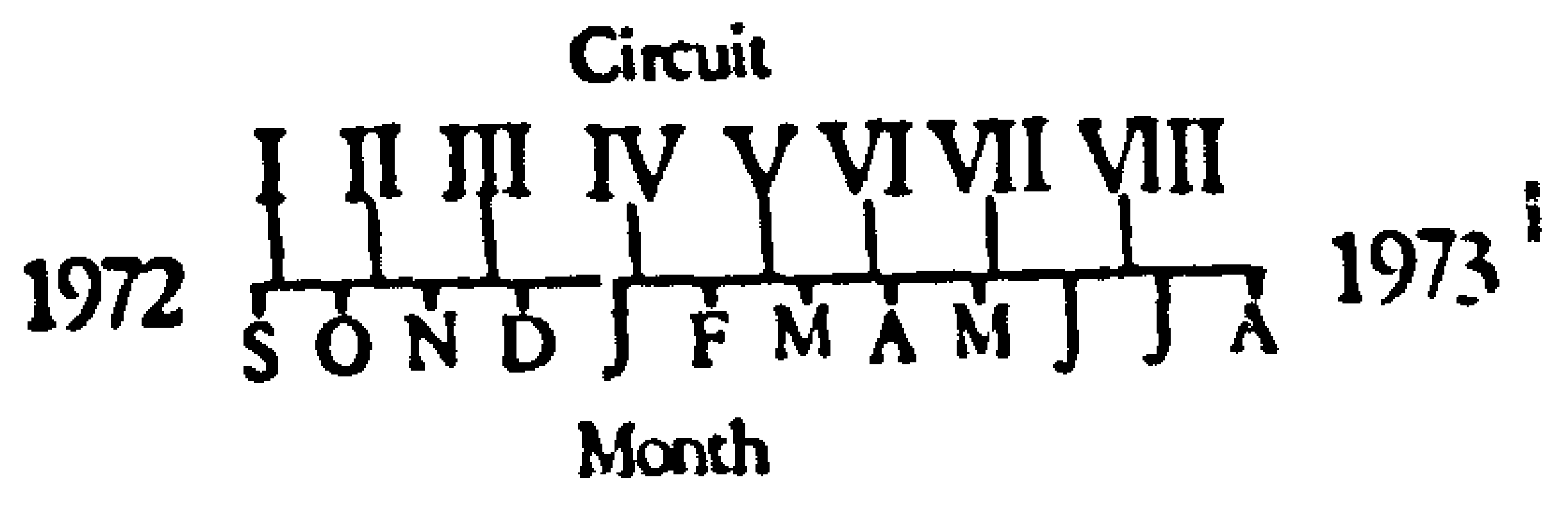
[1] The axillary position of the nipple in Indri is well suited to suckling in these positions.

PLATE 10.3 'Suckling from behind' posture taken by infants over ten weeks of age. The infant of Group V is clasped on the back of his mother in the (locomotive' (or sleeping) position, his neck stretched around her side bringing his (white-crowned) head close to her armpit (where the nipple is situated).

PLATE 10.4 Branch structure in tree often used by infant of Group V for locomotor practice sessions ('rounds'). This type of tree (Symphonia sp), had a great number of regular horizontal branches. I received the impression that the adult female selected these trees to rest in. They possessed the most suitable type of canopy structure for the infant's practice ('rounds').

Figure 10.1 Changes in the mean number of suckling bouts, the % of suckling bouts and the mean number of minutes spent suckling daily by the Group V infant over the year.


Mean number bouts daily
0
1
2
3
4
5
I
II
III
IV
V
VI
VII
VIII
17
22
28
36
42
47
52
59
Infant age (weeks)
% suckling bouts
0
50
100
I
II
III
IV
V
VI
VII
VIII
Mean no. mins daily
0
20
40
60
I
II
III
IV
V
VI
VII
VIII
CIRCUIT


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
1973
Month

lasting a total of 16 - 94 minutes. There were no regular cycles of suckling activity - the infant did not suckle more, for example, on those days following days of poor suckling activity - and it seems likely that the infant suckled outside the period of observation or even, perhaps, during the night.

During those days not adversely affected by the weather, suckling occurred at any time - although it was rarely seen shortly after the group became active or just before activity ceased. When most suckling activity was observed (Circuits III and IV) an equal distribution of bouts across all hours of the active period contrasted with later Circuits when it became restricted to times immediately after the adult female had adopted her final resting position.

Suckling bouts varied from 1 - 41 minutes in duration. The activity was interrrupted only by movement from one breast to the other. The group became inactive when the infant suckled.

Infants aged up to 10 weeks suckled after crawling up the mother's chest to the nipple. Older infants however, climbed on to the mother's back and suckled from behind. From the age of 30-35 weeks weaning commenced, the adult female biting the infant's leg or arm so as to make him dismount. At these times, vigorous short bouts of allogrooming by the infant usually preceded both attempts to suckle and 'requests' for transport (see Section 6). These became longer and more intense as refusals by the mother increased in frequency.

3. FEEDING BEHAVIOUR

A toy-like interest in vegetation is exhibited by carried infants of 6-7 weeks of age. Both the spherical, marble-sized fruit of "tavolo" trees and their leaves were reached for when seen from the mother's chest and sometimes nosed, pulled, bitten and chewed. It is not possible to state with certainty that food was consumed at this age.

Gnawing and chewing twigs, fruit and leaves continues over the subsequent months, but usually as part of a general manipulation of the object which is, at the same time, pulled, twisted, held and observed. The adult female of Group V was seen, when the infant was about 4 months of age, to supply it with "tavolo" fruit which she had herself picked - the only instance of donation observed in <u>Indri</u>. At this age some fruit were definitely consumed as well as being 'played' with but the infant did not leave the mother to obtain the fruit.

At 22 weeks the infant was seen for the first time to leave the mother in order to get better access to food. During the subsequent 6 days of observations the infant ate at least 5 species, one of which was not being simultaneously eaten by the adult female. No consistencies in the type or species of food the infant chose were recognised. It fed on easily obtainable items in trees where the adult female was feeding.

At 28 weeks feeding occurred as part of the locomotor practice activities that dominated the infant's behaviour each day (see Section 4). Considerable amounts of food were consumed, but feeding bouts were all very short.

At this age, food was obtained by the infant from terminal positions in the canopy inaccessible to the heavier adults. All food species consumed by the adult female were eaten by the infant. No estimate could be made of the proportion of time spent feeding by the infant because of difficulties in satisfactorily defining the behavioural category 'feeding'.

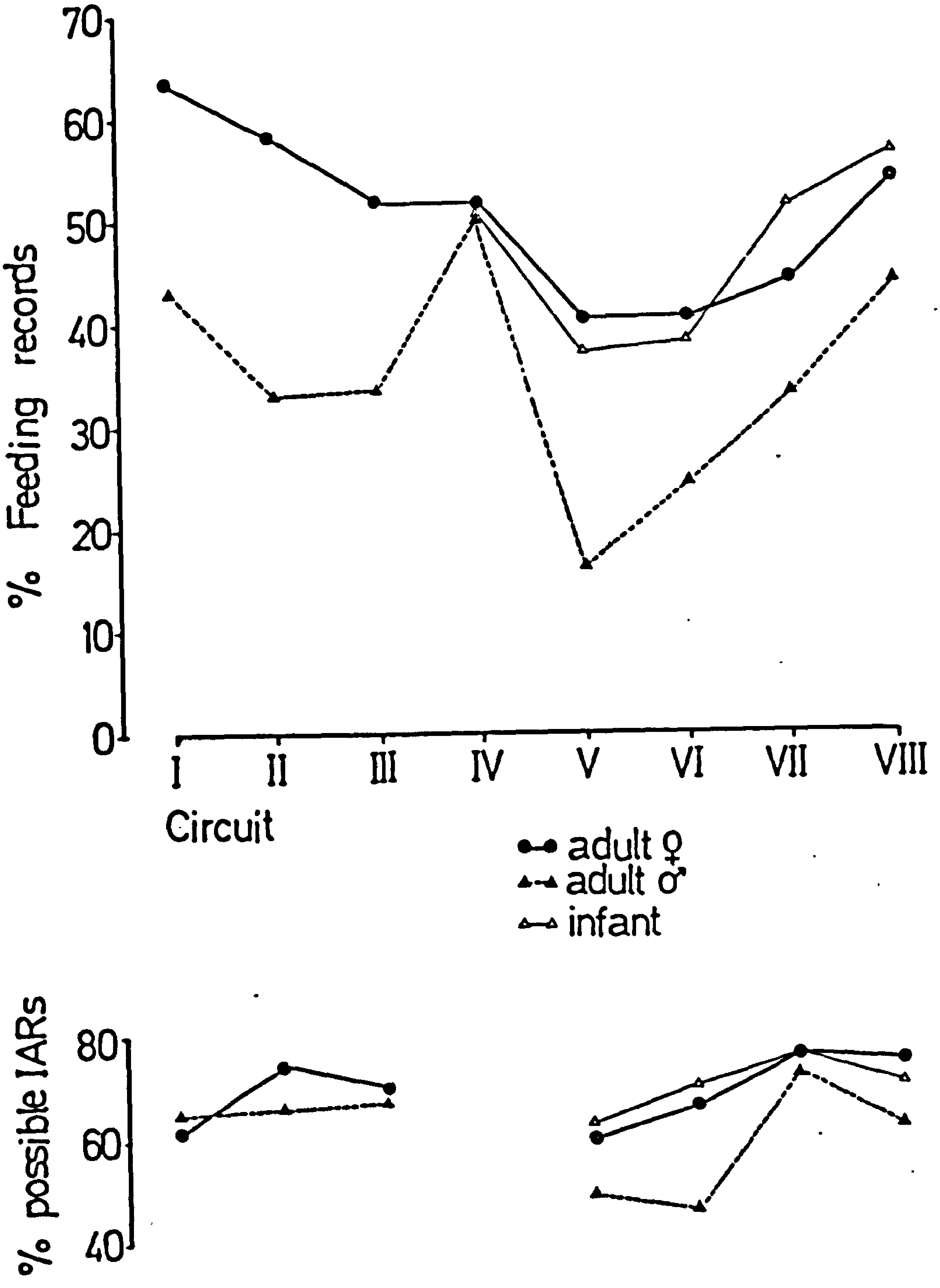
At 36 weeks when feeding occupied over one half (57.6%) of the infant's activity period, there continued to be a lot of movement between short feeding bouts. Feeding postures including suspended 'terminal feeding' positions were, at this age, well developed.

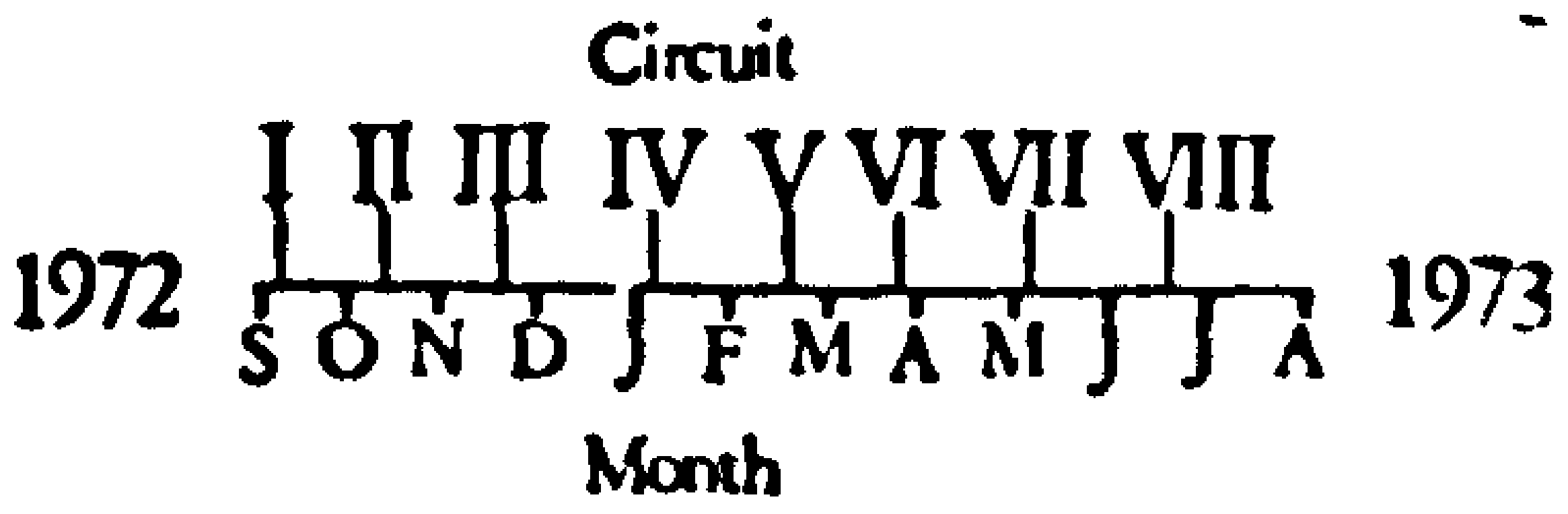
From an age of about 40 weeks the infant's feeding behaviour differed little from that of the adults. The infant was normally seen feeding close to the adult female on the same species and type of food at the same time, but increasingly frequent observations of independent food choice suggested the acquisition of a good knowledge of food plant characteristics.

The infant's activity and position was recorded separately from that of its mother from 36 weeks of age and from an age of 42 weeks until the end of the study the infant fed significantly longer than the adult male during each Circuit's observations (Figure 10.2). The adults frequently waited for the infant to finish a feeding bout before all moving together to a new food source.

In Group P the juvenile, age 16-27 months over the study period, fed significantly more than all other

Figure 10.2 Seasonal and developmental changes in the proportion of time spent feeding by each individual in Group V. Seasonal changes in the proportion of time each individual was seen by the observer are also shown.


% Feeding records
70
60
50
40
30
20
10
0
I
II
III
IV
V
VI
VII
VIII
Circuit
●–● adult ♀
▲--▲ adult ♂
△–△ infant
% possible IARs
80
60
40


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
1973
Month

individuals except her youngest peer (Chapter 6).

4. LOCOMOTION, MOVEMENTS AND POSTURES IN YOUNG INDRI

Repeated observations at intervals long enough for changes in slowly developing behaviours to be easily recognised, enabled the development of the infant's movements to be closely monitored . The initial clambering over part of the mother's chest and neck to gain access to the nipple soon developed into wider and more rapid movements over the whole body. It is unclear exactly when these movements were first extended to use parts of the environment but in the middle of July the first observations of Group V's infant (supposed to be aged 7 or 8 weeks) indicated that this stage had been just reached. It spent much time at this age grasping nearby supports from the female's body and was able to maintain itself in a VCL posture 3-5 cms from her. The infant, carried only on the chest at this age, would move all over the female's body whilst she was resting or feeding. On one occasion the mother jumped to another tree leaving the infant clinging precariously to a vertical branch. She immediately returned and placed the immobile infant on her chest with her hands, licked it twice and then again moved to the other tree. The infant made no attempt to move towards the mother.

The infant did not move from place to place in the environment at this age, and the familiar and safe, graspable medium of the mother was adhered to during any group progression. Observations of reaching for and playing with twigs, fruit and leaves when they by chance appeared near the infant during the female's movements, suggested a developing interest and perception of the environment.

Three to four weeks later, the infant (aged about 3 months) often left the mother's body, grasping small vertical and horizontal branches of up to 5 cms in diameter and moving 10 cms away from the mother. Regular repeated movements between 3 or 4 specific branches began at this age. The infant attempted to jump between these 'station' points, but the movement itself consisted more of a sudden shift of weight and position than a true leap. The grasping facility of hands and feet were well developed at this age, but frictional elements of support were not used in VCL positions. The infant of 3 months was carried on the front or side of the chest - on some occasions slung across the mother's lower back. She never moved to a new tree without the infant.

At the age of 17/18 weeks, elements of the adults' specialised locomotor behaviour (see Chapter 7) were recognised in the infant's movements. The clumsy, grasping proto-leaps performed a few weeks earlier were strung together into a viable 3 or 4 jump sequence, before skills had been acquired for proper leaping or landing on firm supports. The infant clearly practiced the adult 'leap sequence' locomotor system as a whole rather than attempting to perfect skills of its constituent parts. The chosen supports during the leap sequence practice sessions were distributed around a circuitous route, the infant returning to its starting point on or by the side of the mother. These characteristic practice sessions are henceforth called "rounds". During each "round" the infant of this age moved from 2-3 metres from the mother. The supports used varied in diameter from 4 - 10 cms and true jumps of as far as 100 cms were made. Hanging by the arms and other suspended postures were also practised by the infant at this age.

At this stage the infant was carried in both ventral and dorsal carriage positions by the mother. Each practice 'round', coincident with the adult female feeding in canopy positions where a suitable density of small supports existed, ended in jumping on to or near to the mother. On 2 occasions the mother was seen to move away from the infant to another position in the same tree. Once she returned to a position 5 metres from the infant, which then moved towards her to regain contact and tranport. Although the infant spent periods as long as 6 minutes off the mother, he was physically in contact with her for 75% of the activity period. For unknown reasons the frequency of practice rounds varied widely from day to day.

Subsequent observations showed that a very rapid development of locomotor skills was in progress. At the age of 22/23 weeks 'rounds' were rigorously practised every day. Each 'round' took the infant up to 5 metres from the mother, were less circular and ended some feet away from her. Support diameters of 5-15 cms were used and these were mostly vertical in orientation. More time was spent off the female in other activities:

crawling about the canopy and practising postures, frequently hanging by one limb.

The infant of 5 - 6 months was carried mostly on the back of the mother. The mother generally refused to collect the infant, requiring him to move some way towards her to obtain carriage. The impression gained was that forcing the infant to move was of positive educational value and was carefully controlled by the adult female whe waited in VCL 'travelling' positions, observing the infant until he approached her. This behaviour, termed "teaching", frequently upset and disturbed the infant which bleated and whined over difficult jumps or when separated by over 7 metres from the mother. The mother never moved to another tree before waiting for the infant to establish contact and was physically in contact with him for 64% of the active period.

At 28/29 weeks of age, only dorsal carriage was seen. Rounds were, at this age, more ambitious: longer, using larger supports, separated by greater distances and often occurring below the canopy. The number of leaps per sequence during practice rounds however, remained constant. Rounds were occasionally interrupted to pick and consume fruit. Attempts were made by the infant to land on vertical supports of 15 cms in diameter, but these always failed - resulting in falls of up to 30 feet, the dazed infant remaining immobile on the ground for several minutes before slowly climbing back into the canopy. These falls occurred at a rate of 1-3 each day. At this age the infant was able to climb up and down large (25 cm diameter) vertical trunks.

When 'teaching' the mother now required the infant to move between 13 and 27 metres in order to make contact with her, considerable vertical displacements also being necessary. About one third of the attempts to reach the mother failed and she would return part of the way to collect the infant. The infant's skill in landing on large supports (15 cms diameter) was clearly the limiting factor in locomotion.

The infant and mother were physically in contact for 49% of the infant's activity period.

Sometimes between 29 and 36 weeks of age, practice 'rounds' ceased and most of the time off the mother was devoted to feeding activities. It is very likely that these two changes were causally related. The adult female made few or no concessions to the infant, which had to continuously follow her. Except for the first few leaps each morning the infant was never carried at this age as this greatly incovenienced and restricted the movements of the adult female. The infant was in contact with its mother for 39% of the activity period.

Infant leaps of 5 horizontal metres with no loss of height and a firm landing were now easily accomplished. The infant never fell and instead of leaping on to the canopy, sub-canopy vertical landing supports between 10 - 15 cms diameter were preferred. Vertical ascent and descent of smooth tree trunks and the use of arm-over-arm brachial suspension (Plate 10.5) to move from terminal feeding positions back to the main trunk of a tree, were now well developed.

PLATE 10.5 Arm-over-arm movement towards the adult female by the infant of Group V aged 6-7 months.

A significant innovation at this age was the rapidly developing ability to compose suitable arboreal routes. Previously, the infant's optimal or easiest route coincided - presumably because the adult female so positioned herself - with the straight line passage between infant and mother. At 36 weeks of age, no such concession was made and the infant was frequently forced to descend or ascend to suitable, small supports - sometimes moving further from the female in order to ultimately reach her - slowly examining and constructing in advance a satisfactory route. On reaching the adult female the infant sat nearby or immediately began to feed. Limited by the infant's movements, the group at this stage was forced to move slowly about the home range.

At the age of 42 weeks, the infant and adult female rarely touched each other during the activity period. The infant, rather than using different supports, appeared to have learnt, at this age, those supports that could be easily landed on. Route composition was noticeably quicker and the adult female was quickly and economically followed, although different pathways were used.

From 47 weeks only large landing support diameters caused hesitations and difficulties for the infant's leaps and distinguished his movements from those of the adults. These pauses soon disappeared, although large vertical supports were avoided until well into the second year and possibly much later. By the end of the study period the infant/juvenile was able to exactly follow the adult female in about 90% of her chosen arboreal routes, although the tendency to move away from her to feed alone was simultaneously developing.

5. THE DEVELOPMENT OF PLAY

All play bouts in Group V involved the infant and were seasonally restricted to the mid-summer. Of the 14 bouts observed 13 were between the infant and adult male and 1 between the infant and his mother. The infant never initiated play behaviour but briefly wrestled with and kicked the adult male, the latter gently grasping him when he came near. The adult male never approached the infant in order to play with him. Bouts of play were very short and were always terminated by the infant moving away.

The activity itself contrasted somewhat with play observed in Group P. The Group V adult male maintained physical contact with the infant only for very short periods during play, exhibiting extraordinary postures and positions (such as hanging upside down from both legs) near to and sometimes whilst touching the infant (Plate 10.6).

One bout of play was observed when the infant was 22 weeks old, 10 bouts at 28 weeks and 3 at 36 weeks, but this variation reflected essentially the same seasonal distribution found in Group P rather than changes in the infant's development.

6. THE DEVELOPMENT OF ALLOGROOMING

The most frequent overt 'affiliative' activity,

PLATE 10.6(a-h) Sequence of plates illustrating attempt by the adult male of Group V to play with the infant after having briefly groomed it.

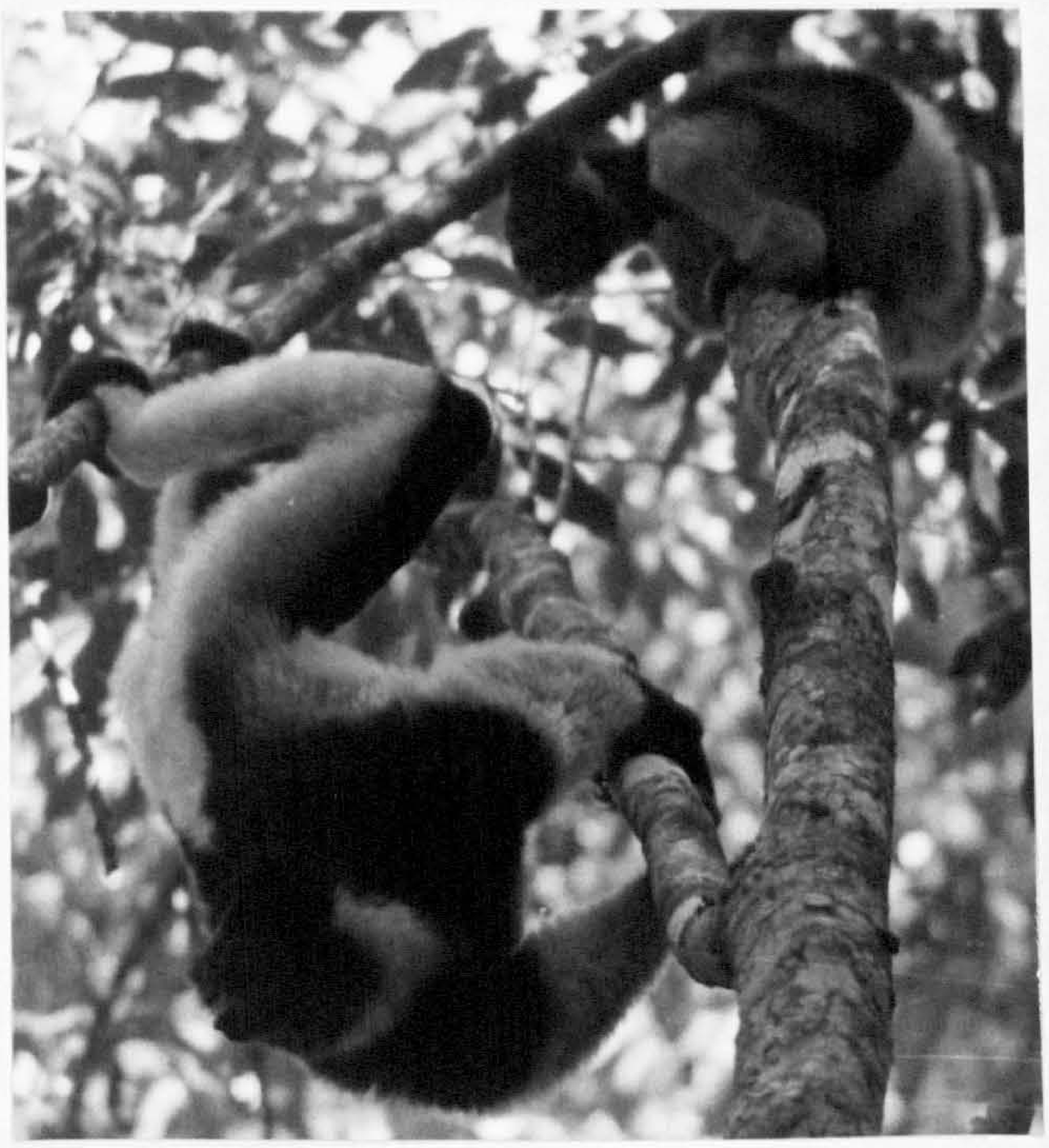
(a)

(b)

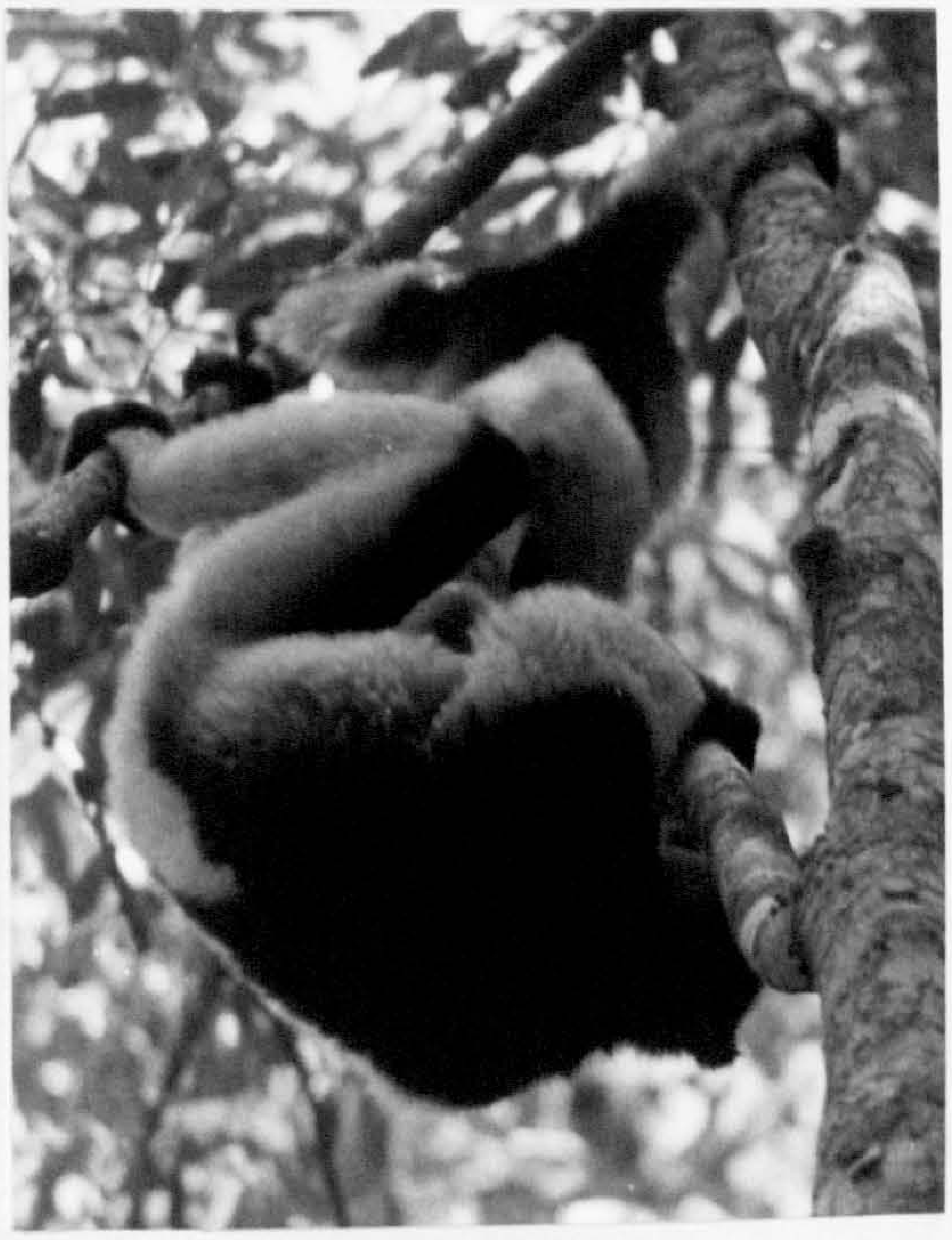
(c)

(d)

PLATE 10.6 (continued)



(e)



(f)

(g)

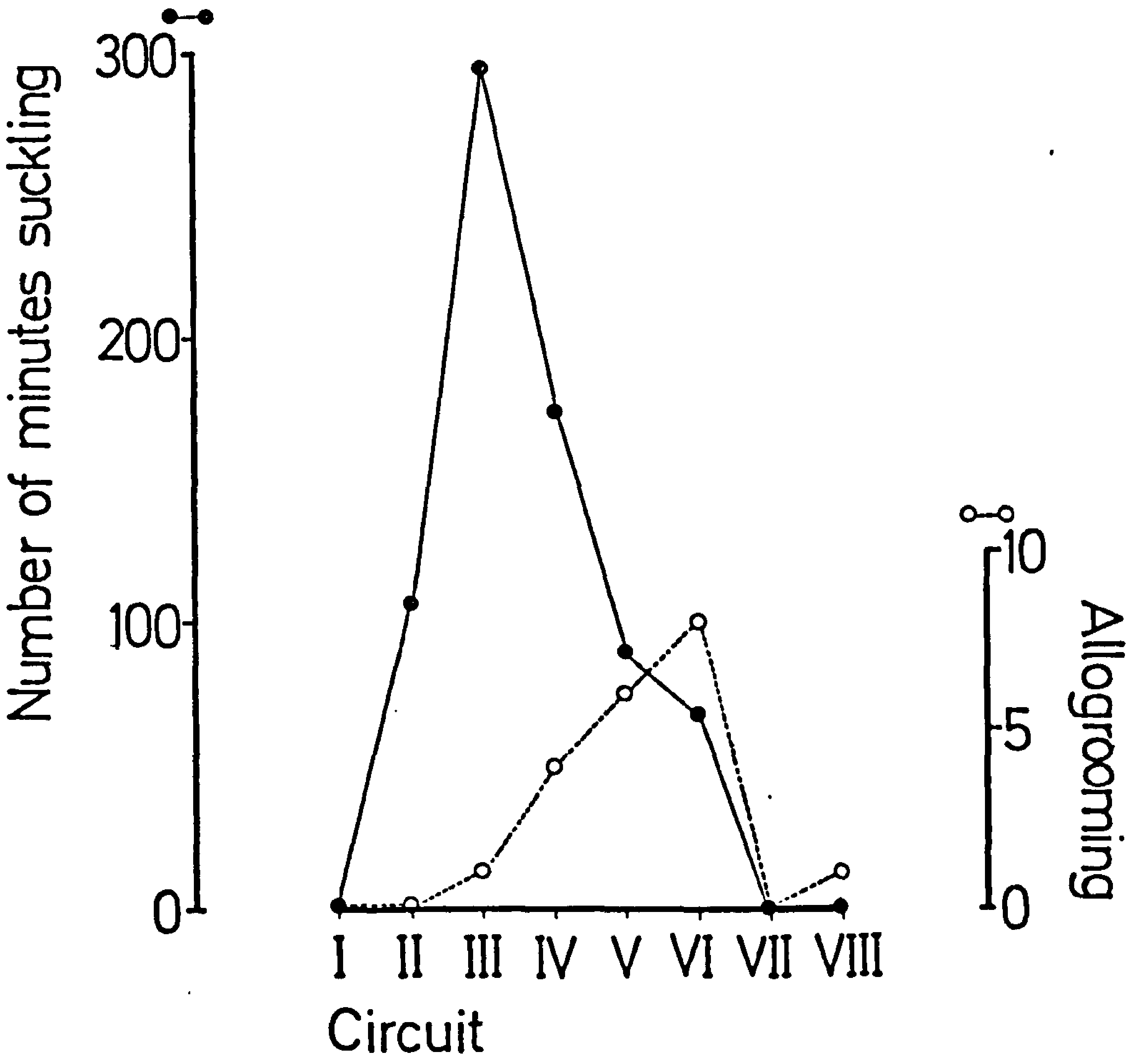
(h)

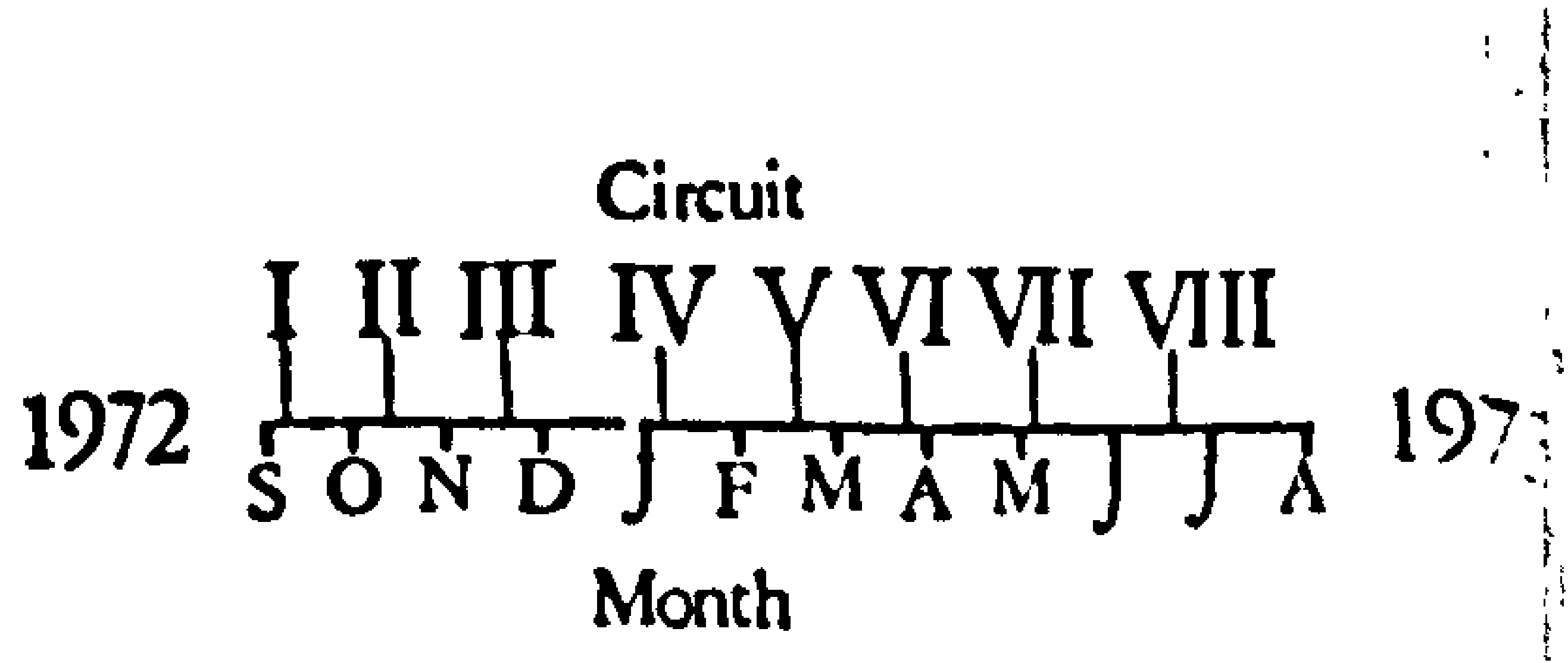
allogrooming, was first performed by the infant at 28 weeks of age. During the whole of the first year the infant only allogroomed the adult female. In Group P the juvenile in its second year rarely groomed any animal except the adult female.

Between 28 and 59 weeks of age, 88 bouts of allogrooming involving the infant were seen. In 20 of these (25%) the infant groomed the adult female. A similar pattern is seen in Group P where the youngest individual groomed others for 30% of the bouts she participated in. The ratio of groomer to groomed (Chapter 8) is greatest, in both groups, for the youngest individuals,3.0 for Group V and 2.2 for Group P.

Allogrooming was used by the infant in Group V to request (i) suckling and (ii) transport from the mother. It was only when these were required by the infant that he was seen to groom the mother in a characteristic and intense fashion for a few seconds. Very often at the time of weaning and when the mother was also refusing to carry the infant, he would clasp on to her back and rigorously groom her neck and back. This would usually be ignored by the female which, before moving, would bite the infant's arm or leg causing him to dismount rapidly. Allogrooming between infant and mother was rarely observed but showed, as expected, a seasonal or developmental trend coincident with the stage of development when suckling and carriage diminished (Figure 10.3).

<u>Figure 10.3</u> Correlations between changes in allogrooming and suckling by the Group V infant throughout the year.


●–●
300
200
100
0
Number of minutes suckling
○–○
10
5
0
Allogrooming
I
II
III
IV
V
VI
VII
VIII
Circuit


Circuit
I
II
III
IV
V
VI
VII
VIII
1972
S
O
N
D
J
F
M
A
M
J
J
A
197
Month

7. THE DEVELOPMENT OF DISPLACEMENT BEHAVIOUR

The infant was never displaced from a feeding position and appeared to have priority over both adults to food. The adult male of Group V avoided feeding near the infant (as he did near the adult female), and the adult female of this group, in a highly localised and small food source, would tend to leave the infant (aged 11 months or more) to feed alone, returning to the food on his departure.

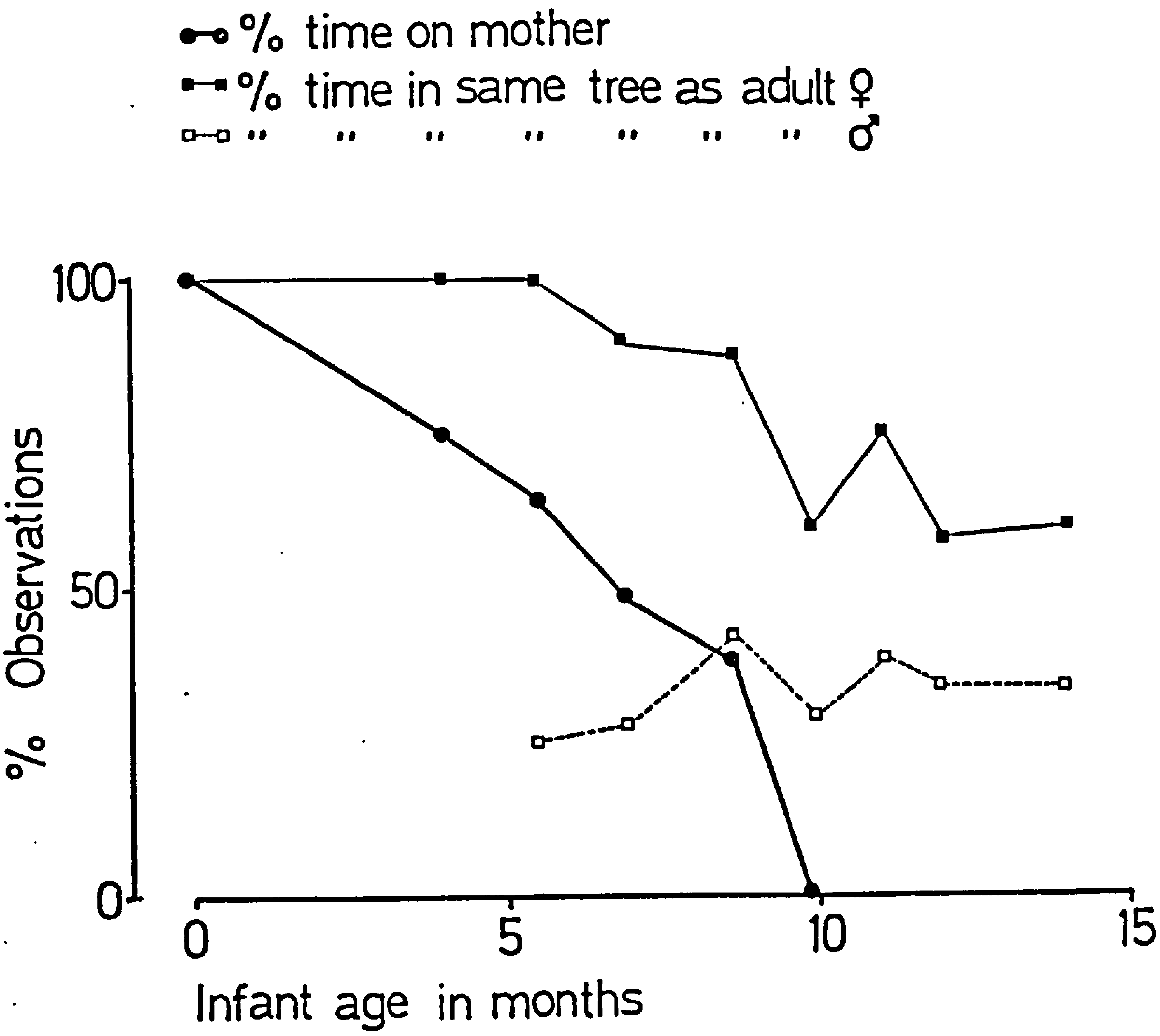
The development of aggressive behaviour was apparent towards the end of the study, although it can not be certain that sitations evoking it had been previously present In Circuit IV the 47-week old infant attempted to displace the adult male for the first time. This observation was repeated 6 weeks later and occurred 5 times during the final Circuit when the infant was aged 59 weeks.

8. INTER-INDIVIDUAL DISTANCES

Until infant Indri are 17 weeks old they are effectively permanently attached to their mother. Over the subsequent 30 weeks this physical relationship diminishes (Figure 10.4) and by 42 weeks the infant only remains in contact with the mother whilst sleeping and, occasionally, during 'quiet periods' (see Chapter 3) which infrequently interrupt the group's activity period.

From the age of 36 weeks distances were regularly recorded between the infant and the adult female. From 42 weeks of age the infant moved 'independently' from (despite still following) the adult female and observations

<u>Figure 10.4</u> Changes in the proportion of time spent by the Group V infant in contact with the mother and in the same tree as mother and adult male, throughout the year.


% time on mother
% time in same tree as adult ♀
" " " " " " " ♂
100
50
0
% Observations
0
5
10
15
Infant age in months

every subsequent 6-weeks indicated no consistencies in the spatial independence of these two individuals (Figure 10.5). Comparison with the distances maintained between adult female and juvenile in Group P suggested that once moving independently, spatial association of the infant with its mother remained close and rather similar from 10 to 24 months of age. Fluctuations in the distance separating the adult female and infant in Group V did not correlate with distances between the adult male and infant (Figure 10.5) and was unlikely, therefore, to have been due to switches in spatial relationships within the group.

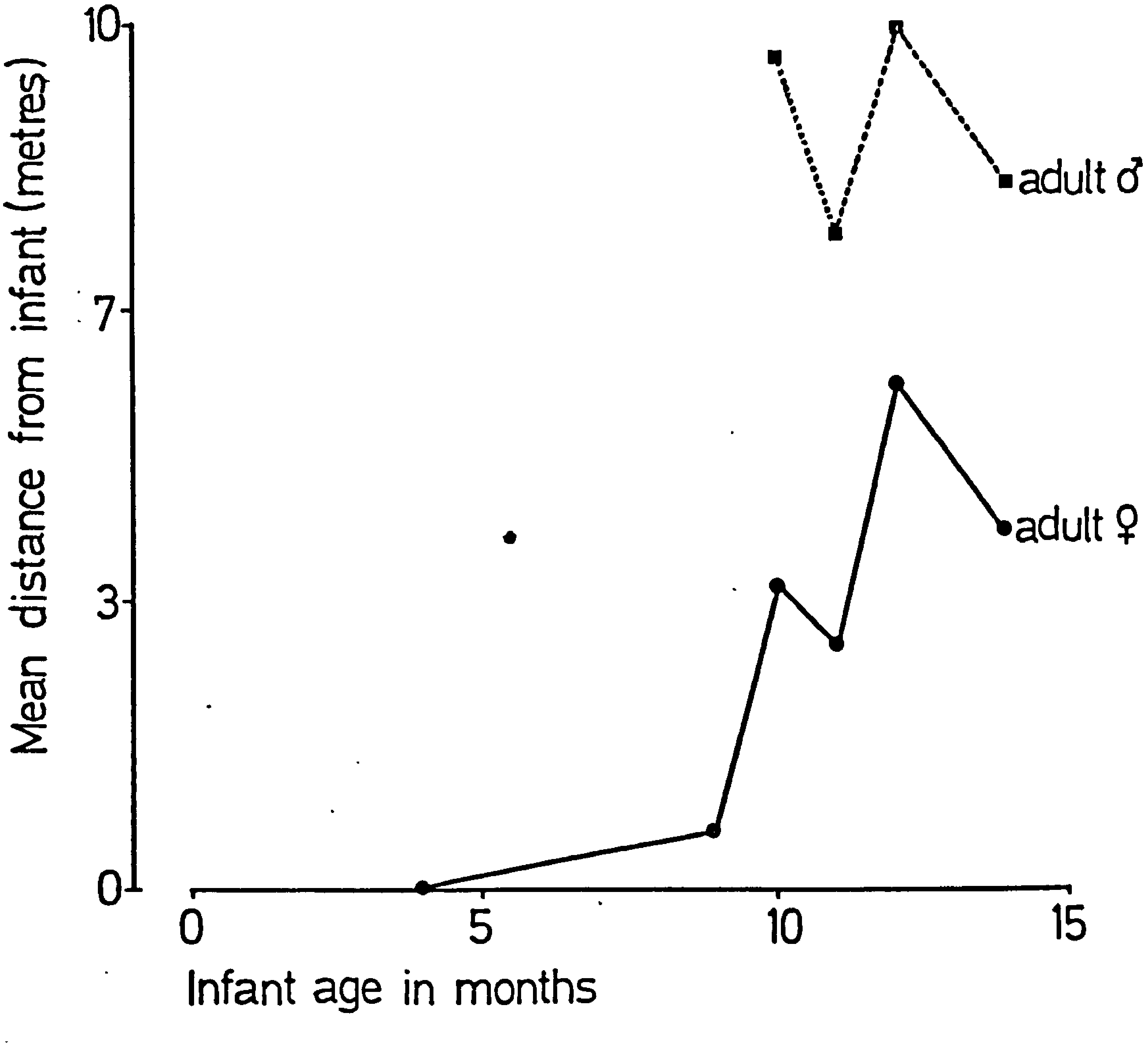
During all periods of observation, the distance between the mother and infant or juvenile aged up to 27 months was smaller than between any other animal for either group.

9. LOCAL SPACING

9.1. Canopy Levels

Once the infant had begun to move on its own, the position of the infant relative to each adult was examined (Chapter 5). Too few data are available over the period 42-59 weeks of age to trace developmental trends in the infant's position. Over the whole of this period, however, (Circuits V-VIII) the distribution of time spent by the infant in various canopy levels did not significantly differ from that of the adult female either for all categories ($X^2_{3df} = 4.63 : 0.2 < p < 0.3$) or for any category considered separately. The infant spent different amounts of time

<u>Figure 10.5</u> Changes in the mean distance separating the Group V infant from (1) adult female, and (2) adult male, throughout the year.



Mean distance from infant (metres)
10
7
3
0
0
5
10
15
Infant age in months
adult ♂
adult ♀

in all canopy levels from the adult male ($X^2_{3df} = 23.35$: $p < 0.001$) and this was largely due to the relatively great amount of time spent by the infant in the canopy ($X^2_{1df} = 16.99$: $p < 0.001$) and the small amount of time spent by the infant outside the canopy ($X^2_{1df} = 4.204$: $0.01 < p < 0.05$).

When only feeding observations are considered, there are again no differences between the positions taken in the trees by the adult female and the infant ($X^2_{3df} = 2.44$: $0.3 < p < 0.5$). Compared to the adult male, however, the infant spent significantly more time feeding in the canopy top ($X^2_{1df} = 8.266$: $0.001 < p < 0.01$) and significantly less time feeding in the canopy bottom. ($X^2_{1df} = 4.538$: $0.01 < p < 0.05$)

These differences in effect mirror those between the adults of this group, with the exception that structural parts of the canopy i.e. canopy bottom, where food is less dense and farther removed from main supports, was used more for feeding by the adult male compared with the infant, but not compared with the adult female.

9.2 Heights

The relative heights of the infant aged 42-59 weeks and the two adults were examined to investigate whether the impression gained of slight but consistent differences was justified from the neasurements taken. No differences were found in categorised height comparisons between infant and adult male ($X^2_{3df} = 1.171$: $0.7 < p < 0.8$),or between infant and adult female ($X^2_{3df} = 2.064$: $0.3 < p < 0.5$).

The relative displacement within height categories was examined by comparing the number of times the infant was higher or lower than the adult female. This analysis showed that when they were in different trees these two animals adopted the same relative height ($X^2_{1df} = 0.48$: $0.3 < p < 0.5$), but when situated in the same tree, the infant was significantly more often higher than the adult female ($X^2_{1df} = 6.88$: $0.001 < p < 0.01$).

Between the ages of 42 and 59 weeks the proportion of time the infant was at the same height as the adult female irrespective of the tree they were situated in, was 35.2% : whereas when they were in the same tree it was 47.3%. In Group P corresponding percentages for the adult female and juvenile (aged 15-27 months) were 42.9% and 55.4%. With the Group P sub-adult (aged probably 3 or 4 years) it was 26.5% and 38.7%. The apparently greater proportion of identical height records for the juvenile and mother in Group P compared to the infant and mother in Group V, is probably an artefact as the relative independence of the Group P juvenile often allowed her to move out of sight of the adult female.[1]

9.3 Situation in the Same Tree

The proportion of observations that the infant and adult female of Group V were in the same tree was too variable to show a trend from Circuit V (infant aged 42 weeks) to Circuit VIII (aged 59 weeks). The greatest difference occurred between Circuit IV and Circuit V,

---

[1] These percentages are expressed as a % of the observations when both animals are in view. The tendency for animals to 'associate' i.e. to be seen together, certainly changes as well.

when the proportion of time these individuals were in the same tree decreased by 40% (Figure 10.4 Table 10.1). The percentage of time that the Group P adult female was in the same tree as the juvenile (aged 15-27 months) was 58.0%..

The tendency for young Indri to be in the same tree as their mother, after an initial reduction as independence in movement is achieved, may vary little for the subsequent 18 months or so. The percentage of observations that the sub-adult of Group P was seen in the same tree as the female was 54.4%.

10. BEHAVIOURAL SYNCHRONY

The most noticeable manifestation of the close relationship between mother and young offspring is the high degree of synchrony, not only in posture and position - but also in activity. Until the age of about 36 weeks however, the activity period of the infant is essentially devoted to specific locomotor skill acquisition (see Section 4), and, therefore, behavioural asynchrony. Following the introduction of feeding activities, the infant has only to feed with the female - on the same items at the same time - to ensure an adequate diet, and the proportion of time these individuals are engaged simultaneously in the same activity therefore increases. Finally following the ability to recognise food, the independence of the juvenile is complete as far as maintenance is concerned and both moving and feeding may occur away from the adult female (Figure 10.6).

Figure 10.6 Theoretical relationships between the synchrony of behaviour between infant and adult female, and infant age in *Indri*.

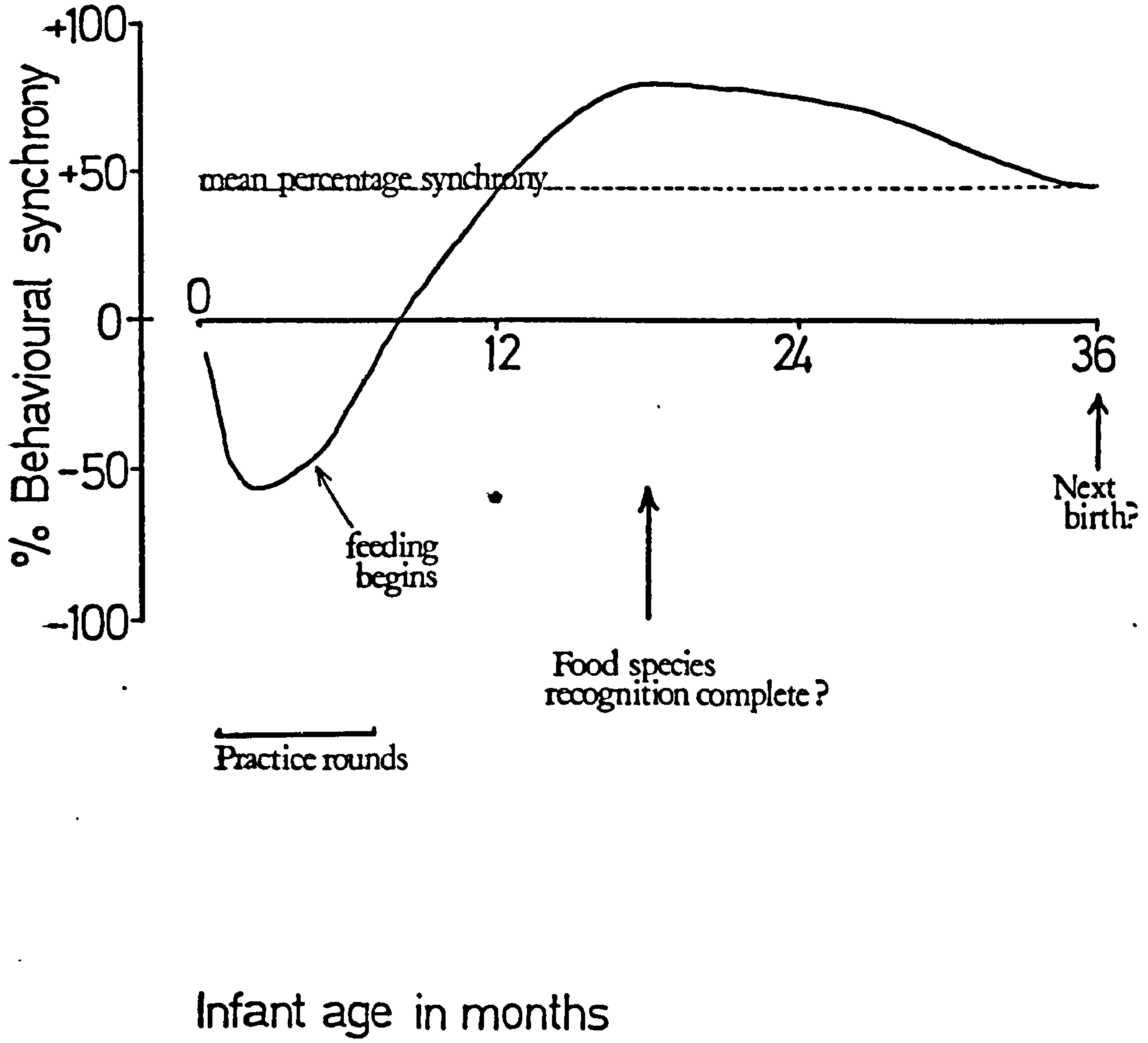

+100
+50
0
-50
-100
% Behavioural synchrony
mean percentage synchrony
0
12
24
36
Next birth?
feeding begins
Food species recognition complete ?
Practice rounds
Infant age in months

Table 10.2 illustrates, over the last 5 Circuits, changes of activity synchrony between the adult female of Group V and the infant for a binary behavioural division of 'feeding' and 'activities other than feeding'. Few changes in the degree of synchrony are of a consistent or developmental pattern over the period for which data are presented. As in other measures of nutritional and locomotor dependence, it is the changes between Circuits IV and V which differ most - twice as much time being spent in asynchronous behaviour in Circuit V compared with Circuit IV (Table 10.3).

The proportion of the infant's feeding records that occurred when the adult female was not feeding clearly illustrates this change, but shows, in addition, a later variability that is hard to interpret (Table 10.3).

Factors other than a developmental trend also affect the changes in social affinity recorded over the year between the adult female and infant. Most changes of a qualitative nature occur in the first 10 months, but great variability may be present thereafter in social distance, the frequency and direction of interaction, the tendency to be in the same tree and behavioural synchrony, all of which may or may not be influenced by developmental parameters. As a rule, little change is advertised over the second year, despite a gradually increasing general independence in movement patterns within the social group, that may be only fully evident when the adult female again attains a reproductive state.

The degree to which infant Indri of up to 12 months

CIRCUIT :	GROUP V IV	V	VI	VII	VIII	GROUP P I/II
	5.0%	20.0%	30.4%	37.9%	18.4%	29.6%

TABLE 10.2.. Proportion of records that infant was feeding whilst the adult female was simultaneously not feeding.

CIRCUIT :	I	II	III	IV	V	VI	VII	VIII
	100%	100%	90%	87.5%	60.0%	75.0%	57.7%	60.0%

$X^2_{(1df)}=2.292$

TABLE 10.1. Changes in the proportion of time mother and infant (Group V) were in the same tree.

	CIRC.	Infant NF Ad♀ NF	Infant NF Ad♀ F	Infant F Ad♀ NF	Infant F Ad♀ F
GROUP V	IV	34.6	7.7	2.9	54.8
	V	49.0	13.8	7.4	29.8
	VI	43.3	11.7	13.7	31.4
	VII	29.0	13.0	22.0	36.0
	VIII	26.2	12.5	11.4	50.0

F Feeding NF Not Feeding

TABLE 10.3. Changes in behavioural synchrony between infant and adult female.

depend on their mother for food, transport, protection, and warmth make the occurrence of annual births very unlikely. Biennial reproductive cycles are unlikely only if this relationship is not adaptable. Physically, the adult female and 20-month-old offspring are in contact only at night and if social huddling of this kind is not essential to the juvenile's health, pregnancy might be expected to occur. Despite following the mother closely at this age, the juvenile could, if necessary, learn about food locations and new food items, by remaining close to other experienced animals. This may have occurred, for example, in Group P during Circuit IV when the juvenile discarded close spatial ties with the crippled adult female and ranged with others every day (see Chapter 8). The dissociation proved temporary as the adult female, her wound healed, slept again with the juvenile during the night and mother and juvenile moved together during the day on subsequent occasions. This seems to suggest that mother-offspring ties at this age may not be physically essential to the offspring's welfare.

11. DISCUSSION

11.1 Play Behaviour

Two distinct forms of play are performed by Indri:

(i) environmental manipulation and practice of feeding, leaping and postures,

(ii) social play involving play-wrestling by 2 or sometimes 3 individuals.

The function of mammalian play is unknown. The most frequently proposed suggestions are:

(a) practice for adult activity. e.g. exercise, muscle tone, correct bone development and muscle attachment, correct innervation and reaction,

(b) learning about the environment. e.g. closer associations with objects in the environment testing the reactions of objects and animals in the environment and learning the range of their behavioural responses.

As observed by Loizos (1967), these are not entirely satisfactory suggestions as play, although predominantly an activity for the young, is also performed by adults.

Andrew (1964) suggests that primate play mirrors the manipulative co-ordinations seen in prey-catching and agonistic behaviour. Sexual actions may also be constituent of play behaviour (Loizos 1967).

The distinction between postural practice and social play holds for all prosimians (Doyle 1974). Locomotor practice of the kind seen in Indri, however, has not been reported elsewhere, although Doyle (1974) describes Galago senegalensis jumping around "... apparently for pure pleasure ..." and similar behaviour occurs in Galago alleni (Charles-Dominique 1971). For Indri the two types of play are age-dependent, social play probably being absent until the infant is 18-months old when the requirements of independent locomotion and feeding have been largely met. Social play at this time may be restricted to the summer months because the more immediate physiological needs are easily satisfied during the longer activity periods at these times of the year (Loy 1970, Bekoff 1972, Baldwin and Baldwin 1973).

Family-living primates, depending on the size and age the group has attained, have differing peer availability for young animals. Thus the infant/juvenile in Group V might be unable to play with a sib before a new infant was 18 months old, when he would be aged 3-4 years. It is presumed, therefore, that social play at an early age is relatively unimportant for Indri's social development.

11.2 Social Grooming

Grooming by prosimians involves the use of the battery of procumbent lower incisors known as the 'dental comb'. Despite Andrew's (1964) assertion that the evolution of the specialised dental array is related solely to the grooming function, this old controversy has been recently revived (see Appendix 3).

The action of allogrooming in primates normally contains fur-parting behaviour and hence requires a degree of manual dexterity that derives from fore-finger/thumb opposability. Sparks(1967) states that infant monkeys do not allogroom and suggests that as opposability is not achieved in Macaca mulatta until about 9 months of age, anatomical limitations may be present (Hines 1942). If the dental 'comb' in lemurs and lorises has evolved for grooming functions it may be relevent to ask if this is related to reduced opposability. The serrated tooth-comb in Galeopithecus, it has been suggested, is functionally adapted to self-grooming, compensating for the impossibility of scratching resulting from the presence of a flying membrane (Wood-Jones 1918). Bishop (1964) suggests the use of the hand by prosimians to be adapted for grooming actions but the hold on fur is one of clenching rather than a fine manipulative parting of a few strands that probably requires true opposability. Opposability is further reduced in the Indriidae (Hill 1953) and no animal during the present study was ever seen to hold or grasp objects or hair between thumb and finger.

The relationship between nipple-searching, hair-parting movements and grooming has been interestingly emphasised by Andrew (1964) who suggests that suckling and grooming may have similar 'reassurance' properties. Freud has regarded human infant suckling and kissing as of erotic equivalence (Kline 1972) and allogrooming, it has been suggested (Michael and Herbert 1963, Rothe 1974, Saayman 1971) is dependent on humoral factors in female monkeys. Certainly allogrooming is very often a constituent of sexual activities and copulatory behaviour in primates.

Observations on Indri suggest that allogrooming is first used as a request for suckling or infant carriage. As these are the only two mother-derived requirements of 7-month old infants, it is not possible to differentiate between specific 'request' behaviour or behaviour related to general appeasement in its motivational origin. Due to the difference in contexts and the poor (if existent) influence the action has on the behaviour of the mother - she virtually always displaced the infant anyway - it appears that 'appeasement' is a more satisfactory interpretation of the infant's motives in performing this behaviour.

Reassurance or appeasement could explain allogrooming interactions in Group P - especially in individuals widely separated in the feeding hierarchy. Thus those pairs of individuals where one partner (A) allogroomed the other (B) more than vice-versa, were also the pairs in which B displaced A more than A displaced B (see Chapter 8). Appeasement does not explain the <u>frequency</u> with which individuals allogroomed, however, and more particularly it does not explain the large numbers of bouts of grooming (25.5% of all the bouts seen) between the adult female and juvenile (aged 15-27 months) in Group P - individuals which were of equal, top rank in the feeding hierarchy.

11.3 Conclusion

Whether or not VCL locomotion is a specialised or ancestral primate characteristic (Walker 1967, Charles-Dominique and Martin 1970, Cartmill 1972) the development of this form of movement in young <u>Indri</u> requires constant and often dangerous practice.

In several ways the early development of <u>Indri</u> is a race against time. The animal must learn to move before it becomes too big to be carried and learn to feed on vegetation before suckling terminates. At one critical time for the group the infant is too young to move rapidly and too large to be carried. <u>Indri</u> groups with infants at this stage were found on 3 occasions. Although other group members fled the infant remained motionless and could be easily approached to within a few feet. It is at this stage of development that predators (if they exist) might act, and it is obviously to the advantage of the individual that such a stage be short-lived.

Once the infant has become an essentially independent individual, the rate of development slows and may take up to 9 years to complete (see Chapter 4).

12. SUMMARY

1. The development of young Indri was traced from birth to over 2 years of age by observations on three young animals. Suckling lasted for about 12 months. Feeding on solid foods began at 30 weeks of age and the infant was always carried by the mother for the first 6 months. From the age of 3 months the infant's main activity was locomotor practice. From the age of 9-10 months the infant always moved without the aid of the mother and fed for longer periods of time than both adults. The ontogeny of locomotion was clearly organised through practising complete sequences of movement from the beginning, rather than learning elementary skills and later stringing them together. The behaviour of the mother was instrumental in encouraging the infant to learn how to move and compose its own arboreal routes.

2. The use of allogrooming by the infant as a request for suckling or carriage from the mother is suggestive of its role in adult or older Indri. From an early age the infant was dominant in feeding situations over all other animals, but no aggressive behaviour was exhibited during the first year. The average distance between the mother and her young offspring was very low for the first two years. Over this period of time these 2 animals were usually feeding, resting and sleeping together. Within the same tree the infant was often found feeding higher than the adult female in positions where its low weight was at

an advantage.

3. The social environment of nuclear family groups varies according to their developmental stage (i.e. age). Thus, the offspring born to a newly mated pair spends its first 2 or 3 years without sibs. It is presumed that the inability to play, groom and otherwise interact with sibs is inconsequential in subsequent development.

CHAPTER 11

General Discussion

1. THE APPROACH

Difficulties encountered in observing animals in the dense vegetation of the Malagasy rain-forests made contact with an Indri group hard to maintain, and biased records of their behaviour towards conspicuous activities. Most primate field studies in similar environments have met comparable problems of observation (Aldrich-Blake 1970, Chalmers 1967, 1968), although few have discussed its effects on recorded information and still fewer have attempted to measure its importance (for an exception see Clutton-Brock 1974a).

It is particularly problematical to establish the nature of spatial relations between primate group members when only a small proportion of the group can be seen at any one time. And yet the position and activity of each animal must be related to the behaviour of other group members in order to measure the inter-dependence of behaviour in the group ('social organisation'). This critical feature of society is more clearly recognised when such inter-dependence (which results from communication) can be shown to exist without any obvious interaction (signal, vocalisation or contact) between group members. This, it should be emphasised, is a minimal form of approach as the development of social behaviour - the changing social influences on a growing individual - are ignored. Under field conditions, however, a single observer in a visually impenetrable forest is much limited in what behaviour can be recorded in a short space of time.

When one is faced with the problem of isolating one variable (animal behaviour) from two inextricably entangled together (animal behaviour + observer behaviour), it is expeditious to fix one (observer behaviour) and record the other. Thus rules were adopted in this study to fix the behaviour of the observer by making it a function of that of the animals. The behaviour (position) of the observer was, therefore, a reflection of animal dispersion and could indeed be recorded as such, to examine, for example, changes in the spread of the group over the research period.

The system adopted in this study had a major additional advantage in that the tendency not to see animals was also informative about the animal's behaviour. In situations where on average each individual was more often not seen than seen this is of obvious value. On reflection, the regimentation of the observer's behaviour could probably have been of more use than was made of it. Had the reasons been noted why an animal could not be seen (e.g. animal moved away, moved behind a tree, observer forced to move nearer another animal), then some positive measure of the animal's state of habituation to the observer and a better idea of group dispersion could have been obtained.

The imposition of strict disciplines of observer movement are not suitable for all forest-living primate studies. Where group size is large, animal behaviour too variable or rapidly changing, or where animals are excessively dispersed, the observer must be more flexible in his reactions. It is worth noting, however, that for prosimians which live in small aggregations with relatively limited behavioural repertoires and nocturnal habits, it may be considered useful to define the behaviour of the observer in order to obtain most information about the activities of the animals.

Use of modern techniques of sophisticated telemetry, light intensifiers, or by multi-observer or capture studies, enable difficulties in recording nocturnal primates' behaviour to be somewhat mitigated; but these are not always practical alternatives.

Standardisation of techniques for recording animal behaviour in the wild are long overdue. Differences encountered in information published on howler monkeys (Bernstein 1964, Chivers 1969, Richard 1970) and red colobus (Clutton-Brock 1974a) probably derive from observers' different definitions of behavioural categories, different techniques of recording information and, possibly, different movements and attitudes. The method adopted in this study could be applied to other species living under similar conditions.

It is believed that the data recorded during the course of the study satisfactorily represented the animals' behaviour as attempts were made to examine the behaviour of non-sighted individuals and compare it with that of the sighted individuals, by using a second observer. Although this test was not executed on all individuals it seems likely that no individual behaved differently when out of sight of the observer from when it was seen. Comparing the behaviour of different forest-living primate species requires such a check to be made - not because an assumption that the observer does not affect the animals' behaviour is necessarily invalid, but because it is impossible to know how reasonable such an assumption may be. In this study only the proportion of time spent by individuals and groups in feeding activities is extensively employed, and as comparisons were made between individuals or groups and biases were probably equal for all animals, any non-representative recording did not influence the conclusions drawn.

The small group size, the habituation of the animals to the observer, and the standardisation of observer behaviour permitted a large proportion of the behaviour (on a point-sample calculation) of the study groups to be recorded. This permitted a relatively fine degree of analysis of topics such as intra-group dispersion, feeding synchrony, and food choice stochastics. The choice of a lemur species for reasons outlined in Chapter 1 - low frequency of behavioural change and small repertoire of different activities - was supported by the detailed information obtained. The use of the recorded information, however, is somewhat limited by the failure to observe a full mating season (see Section 3), and the restricted periods of time during which quantitative data were obtained each Circuit.

2. THE RESULTS

2.1. Differences Between the Study Groups (Group P and Group V)

The original aim of this study - to compare and contrast the behaviour and ecology of Indri groups of different sizes - became extensively modified to form the less ambitious project of a full description of Indri behaviour. Generalisations made about Indri in previous chapters have relied largely upon the representativeness of the two main study groups at Analamazoatra (Group P and

Group V). Some differences between groups may, however, have been related to the groups' different ages[1] according to the duration that they had occupied their home ranges. The process of the 'growth' of Indri groups (with increments of successive offspring supposedly every 2 or 3 years), the presumed departure of mature offspring, their acquisition of a mate and appropriation or formation of a territory, all remain unknown. In siamang one mated pair has been seen to form a ranging area adjacent to the home range of a group from which one of the animals (a sub-adult male) derived (Aldrich-Blake & Chivers 1973). If unfamiliar parts of the forest are occupied by mated pairs of Hylobates, Symphalangus and Indri, great contrast should be evident to an observer in the way in which such 'groups' range and feed. One might expect animals unfamiliar with their environment ('inexperienced groups') to differ behaviourally from those familiar with their environment ('knowledgeable groups') in the following ways:

(1) Inexperienced groups' ranging behaviour might incorporate a higher proportion of searching/foraging activities.

(2) Inexperienced groups might locate and revisit large supplies of food whilst diversifying their diet in small forays about the ranging area, until the distribution of foods had been slowly learnt. Knowledgeable groups might be expected to choose more within species and be more wasteful when feeding.

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[1] The 'age' of a group is the length of time that its reproducing adult male and adult female have ranged together in the same area. At present, because Indri reproduction and group genesis have not been observed, it remains a somewhat hypothetical construction.

(3) Inexperienced groups might be expected to feed more slowly (perhaps be active longer each day) and spend different amounts of time feeding in different parts of the home range. The time spent feeding may be more variable across months in inexperienced groups than in knowledgeable groups.

(4) Diversity of diet, if essential, might be assumed continuously and locally by inexperienced groups, whilst knowledgeable groups might be expected to travel to assured food supplies on longer more predictable cycles.

(5) Knowledgeable groups might move to different parts to engage in predetermined activities. Therefore it is more likely that inexperienced groups would occupy some parts of the home range for short periods of time.

(6) Social relationships may be more strained or aggressive, and 'dominance' enforced in situations where food is less 'available' i.e. its location less well known.

(7) Territorial borders of inexperienced groups may be less clearly defined and require a more regular and/or more frequent defence.

In <u>Indri</u> and the hylobatids those groups occupying unfamiliar home ranges may be those groups which consist of a newly formed pair or a mated adult pair with their first infant. Group V at Analamazoatra was of this composition and, according to local people, had not been long in the area. Several features of the behaviour of Group V supported the contention that they possessed a poorer knowledge of their home range than Group P:

(1) Group V was consistently active longer each day until the end of the study, when their activity period did not differ from that of Group P. Group V spent a smaller proportion of time feeding per hour of activity than Group P.

(2) The proportion of time spent feeding varied more between periods of observation (Circuits) in Group V than in Group P. Group P was more selective in its choice of foods within plant species than Group V.

(3) The amount of time spent in a quadrat each time it was entered was proportional to the frequency of entry to that quadrat over the year for Group V but independent of this frequency for Group P. Thus Group P gave the impression of entering different quadrats to engage in specific activities, whilst Group V sometimes did not.

(4) Group V moved about 3 times as far as Group P when moving from one quadrat to another. As Group P moved in straight lines or wide arcs this meant that Group V was moving sideways in "local movements" that appeared to permit them to visit more trees, examining, perhaps, a greater number of potential food sources. Furthermore Group V tended to make more angled turns the less they fed, suggesting the local movements were, indeed, related to feeding behaviour.

(5) The relationship between the adults of each group suggested that those of Group V were in a more competitive social situation than those of Group P. Thus

the Group V adult female exerted her dominance in feeding situations by aggressive displacements of the Group V male to a lower (less profitable) feeding situation. The Group V adult male fed less, fed on poorer foods, took second choice at feeding sites and located foods for the adult female in Group V. This form of relationship between the adults was not so obvious in Group P.

(6) Group V appeared to be less selective than Group P in its choice of sleeping sites.

The observations of Aldrich-Blake & Chivers (1973) show some striking similarities to those reported here. The new ('inexperienced') group formed by the sub-adult male from a neighbouring group, one young female and one old female, was found to be active significantly longer each day, moved in less coordinated movements between food sources and ranged over a wider area than their knowledgeable neighbours.

Two features of the behaviour of Group V which, when compared with Group P, argued against the hypothesis that Group V was relatively unfamiliar with its home range:

(1) Group V, like Group P, fed equally in all parts of the home range, irrespective of whether those parts were frequently or infrequently visited or if little or much time was spent in them. This could be simply explained, however, had Group V successfully avoided those parts of the home range where food could not be found, moving rapidly on to other areas. It is rather

more likely that Indri in an unfamiliar region would quickly scan the forest for food and move on to another part of the home range rather than examine each area in minute detail, as heterogeneity in the forest - both in species complement and phenology - was so extensive.

(2) Group V might have been expected to return more frequently to areas they knew contained food. Measures of the frequency with which quadrats were re-entered would then have been greater for Group V than for Group P. No alternative explanation for this finding can be offered but the peculiar geometry of the home range - dumbell shaped - may have affected their ability to return quickly to areas rich in food.

It should be emphasised that the hypothesis which is tentatively proposed to account for differences between groups is suggested only as a reasonable basis on which to consider most, if not all of the major differences in feeding, ranging, and social behaviour. In no way dissociated from the purported differences in 'familiarity' with the home ranges demonstrated by the two main study groups, are the differences in group composition. Thus, the presence of an infant may alone have accounted for a need for a greater dietetic diversity, requiring the animals to search wider for food and may have caused an extension to the afternoons' activities so that more food could be consumed by the lactating adult female. Furthermore, differences in the distribution of food (although these were not obvious) may have caused differences in home range utilisation and ranging behaviour.

Neither of these alternative explanations, however, fit the facts as tightly as the first. The presence of an infant, for example, does not account for the following characteristics of Group V:

(1) the variability in the amount of time spent feeding between successive Circuits,

(2) the lower proportion of time spent feeding throughout the day when infant suckling had ceased,

(3) the variation in the amount of time spent in a quadrat each time it was entered,

(4) the local ('searching') movements within quadrats,

(5) the relationship between the frequency of angled turns and the proportion of time spent feeding.

Differences in food distribution does not account for (1), (2), (4) and (5) above, and in addition, is not supported by differences between groups' activity period duration or social behaviour.

Adaptive qualities of primate feeding behaviour can not be fully understood unless some measure of the amount of food 'available' to the animals is obtained. Measures of food availability for arboreal primates have been calculated from plant species density and qualitative observations of leaf or fruit presence (Richard 1973), estimates of food density within trees and the trees' canopy cover (Hladik & Hladik 1972) and measures of species density and canopy surface area (Clutton-Brock 1972). However, what seems to be 'available' to primates may in fact be denied them. For example intra-specific variation in the presence of toxic compounds, parasitic infestation, and the digestibility of plants may considerably alter their nutrient value but remain to the observer's eye 'available' (Freeland & Janzen 1974, Struhsaker 1975). Furthermore food may remain 'available' for only short periods of time. In the Malagasy rain-forest a flock of parrots or pigeons could consume all the fruit in a tree also fed in by Indri (and other lemurs) within a matter of minutes. During the Indri study no criteria could be resolved to clearly identify potential food, and difficulties in plant species recognition prohibited attempts to measure food species density and distribution. A further study is required to examine the problem of how Indri learn what to eat and how they accumulate knowledge about the distribution of food. Such a study would certainly necessitate recording parameters of food 'availability'.

2.2. Social Relationships in Indri

In few primate field studies have all or most group members been identified (but see: Jolly 1966, Mizuhara 1964, Richard 1975).

The small group size in Indri permitted studies to be made of differences between each dyadic relationship. Those features which were compared: the tendency for 2 individuals to be seen in the same scan of the group or in the same scan and in the same tree; the distance separating 2 individuals; the frequency with which 2 individuals interacted in various ways; differences in individuals' behaviour when near or far from others, allowed each relationship to be clearly distinguished from the others. A higher order examination of Indri society viz. how some relationships influenced others, was not made, except for an investigation of the differing tendencies for 2 animals to be close together in the absence or presence of other group members nearby.

Adult females and young animals were found to be at the top of a 'feeding hierarchy', adult males and old offspring at the bottom. Much of the interaction occurring within Indri groups was seen to be unobtrusive (see below) but social behaviour involving contact was more frequently observed in low ranking than in high ranking animals. The 'dominance' of adult female Indri was manifested in several ways:

(1) freedom of movement around a food source without incurring aggression from group members,
(2) ability to displace any other individual from its feeding or resting position,
(3) being avoided by some other individuals when feeding,
(4) apparent control of adult male's feeding behaviour by the adult female in:
    (a) the timing of feeding
    (b) the amount of time spent feeding
    (c) the position in trees where the male fed
    (d) 'influencing' the male to obtain second choice of food by his feeding in the exact positions vacated by the female after she had fed.

Indirect effects of female dominance which may also have been an important constituent of the relationship with the adult male of the group were:

(a) The greater amount of time spent feeding by the adult female compared to the adult male,

(b) the adult male feeding on less nutritious foods than the adult female,

(c) the adult male feeding relatively less than the adult female at times of the year when the group as a whole fed least,

(d) the adult male (but not female) feeding least at times of the year when most angled movements of the group were being taken.

Female dominance over males is rarely observed amongst primates. Except for instances where several females 'gang up' to displace males (Wolfheim & Rowell 1972), consistant dominance of females over males is restricted to the Lemuroidea[1] (Jolly 1966, Richard & Heimbuch 1975, Budnitz & Dainis 1975, this study). Although it appears to be widespread, female-dominance is not universal in lemurs as no obvious indication of rank-ordered relationships could be found in Lemur fulvus either by Sussman (1975) or by Harrington (1975).

During this study on Indri many lemur species were found to inhabit the rain-forests of eastern Madagascar at low concentrations. A close relationship, it was suggested, exists between the number of species of plants and animals, the density of particular species of plants and animals and the rate of reproduction of both plants and animals. Although food abundance was not estimated, Indri show a particularly high degree of selectivity for young foliage compared to other

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[1] However Charles-Dominique (1972) suggests, from observations made on allogrooming in Galago demidovii, that females behaved as though they were dominant over males.

folivorous primates (Hladik, C.M. pers. comm.) and this may be limiting their population density. If food was, therefore, in restricted supplies feeding dominance of the kind illustrated by Indri might afford a more optimal system of food distribution within the group in favour of the pregnant or lactating adult female[1]. Although in other species of primate great food selectivity may require large home range (Clutton-Brock 1975a), the size of a territory is likely to be limited by the abilities of the group to defend it.

The incidence of adult female dominance in lemurs is probably too widespread for a species-specific interpretation (above) to be fully explanatory. Its independent discovery in 3 species makes it an issue of major interest, and is suggestive of factors other than 'hierarchy' being of central importance in the social structure of the haplorhine primates (see Section 3.2). Attention should now be drawn to examination of the relationship between group composition (including sex ratio), physical sexual dimorphism and sex-dependent 'dominance' in lemur groups. Only with demographic information of this kind can ecological differences between primate species be understood in reproductive terms (Crook 1970, 1972).

2.3 Communication in Indri

Although Indri, as a primate, engages in social interactions such as allogrooming, playing, displacing and

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[1] This hypothesis does not require an assumption of 'group selection' - see Section 3.1 .

wrestling, these are infrequent. Intra-group vocal communication, perhaps to be expected in primates inhabiting dense forest environments (Struhsaker 1967, 1969) is rare, and behavioural displays within the group infrequent if not altogether absent.

Nevertheless it has been shown that the lack of overt forms of social communication did not mean that animals did not closely monitor each other's positions and activities and alter their own behaviour as a result. Information has been presented that Indri group members:

(1) Differed individually in choosing parts of the trees they rested in and parts of the trees they fed in. The adult females and young animals of both groups, for example, fed consistently higher than the adult males and old offspring. Higher parts of the trees probably contain more food than lower parts.

(2) Fed in different parts of the trees according to which animal(s) was/were nearby or in the same tree. The adult male of each group avoided more than any other animal being at the same canopy level as the adult female.In general, the presence nearby of the adult female and young animals appeared not only to influence the height of other individuals (which moved lower) but also to inhibit their feeding activities.

The social consequences of one group member being near to another did not necessarily account for all the differences found between individuals' feeding positions in the trees, as some (lighter) animals could exploit some foods better than others. Examination, however, of distances separating adults when either or both were feeding confirmed--especially for Group V - an inhibitory effect on the male's feeding activity by the adult female, mediated (apparently) through inter-individual distance. It was generally found to be those animals which normally stayed farthest apart which were most influenced by each other's behaviour when they were close together.

Small inter-individual distances (IID) between two members of a primate group has often been taken as a measure of affinity in their relationship (Carpenter 1964, Ripley 1970) and the same could be said of those relationships observed in Indri. However, the potential frequency of interaction between group members can not necessarily be predicted by measures of mean IID (Wilson 1972) for two reasons:

(1) This requires complete data. In an environment of poor visibility the distance between two animals when one or both is/are out of sight may be important. In this study IID's could not be determined for 80% of the time.

(2) The distributions of distance separating two individuals may not be normal. Thus, as for the relationship between 02 and the Adult ♀ in Group P observed in this study, two animals may either remain far apart or very close but not at intermediary distances (cf. 'average spacing' of Carpenter 1964).

The analysis of spatial relations in Indri, therefore, suggested that in addition to the non-applicability of the 'random movement model'[1] the distance separating any two individuals could not be described in the form of a simple

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[1] 'The random movement model' of individual dispersion within a group is the model in which all group members move randomly with respect to each other whilst moving as a unit around the ranging area.

equation (Kummer 1974).

In this study measures of concordance between classical interpretations of 'affinity' in the relationships observed i.e. grooming direction and frequency; aggression direction and frequency; inter-individual distance; 'association' frequency, were high only because of the constituent top-ranking adult female/infant relationship. If this relationship was omitted from the correlations there was no significant agreement between the different measures. A similar finding was reported by Gartlan (1968) for Cercopithecus aethiops (using, however different classes of social interaction) and, perhaps more significantly, by Richard (Richard 1973, Richard & Heimbuch 1975) for Propithecus verreauxi.

'Family-living' primates offer a good opportunity for studies of the similarity of specific relationships such as adult male/oldest offspring or adult female/adult male in relatively constant social environments, as there is no more than one member of each age/sex class in each group. This requires, however, a study of sufficient length to precisely record the behaviour of at least 3 and preferably 5 or more 'family' groups.

Indri is a noisy primate. Although most primates are capable of communicating over long distances by means of loud calls, regularly emitted, infectious calling sessions - in which a whole population participates - are probably restricted to the Hylobatidae, the Colobinae, Alouatta, Callicebus and Indri. The function of these calling sessions and the benefit of calling to individual groups is uncertain (but see Chivers 1969, Waser 1975), especially if it appears to evoke an inter-group encounter (Mason 1966, Ellefson 1968). No certain function could be attributed to relaxed, morning vocal exchanges in Indri. Communication between primate groups is of particular interest (Wynne-Edwards 1962) and a fuller study using two (or several) observers with playback equipment, for a period that includes a reproductive season, should be enlightening.

3. THE IMPLICATIONS

3.1. Social Organisation Amongst Animals Including Primates

Interpretations of the adaptiveness of animal societies fall naturally into two groups: those in which animals are considered to benefit individually by living in some form of close-knit social structure and those in which the whole group may profit from such an organisation. Models of the latter variety require the concept of 'group selection' (Wynne-Edwards 1962) to primarily account for their evolution. As selfish behaviour profitable to an individual would be selected for within the group, problems arise in the maintenance of social organisations which have arisen in this way (Maynard-Smith 1964, Williams 1966). Where individuals alone are seen to benefit from group living the maintenance of society is to the advantage of all its constituents ('reciprocal altruism') and problems concerning the fate or fortune of selfish individuals do not arise (Trivers 1971)[1].

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[1] The effects of individual and group selection coincide, however, where members of a group are genetically related ('kin selection') and it is to the advantage of each individual that other group members reproduce. This concept has been expanded to account for the independent evolution of complex societies in the Hymenoptera (Hamilton 1964).

Although the relative importance of 'group' and 'individual' selection in the evolution of animal societies is a matter of controversy, the majority of authors consider it likely that intra-specific competition is of most importance at the individual level.

Too little is known at present to accurately identify the advantages that living in groups confer on individuals. In some cases aggregation may physiologically alter the environment (Allee (undated), Oppenheimer & Lang 1969), permit individuals to hunt or defend themselves better (Vine 1971, Hall & DeVore 1965, Goss-Custard et al. 1972), locate reproductive partners more easily, or obtain food more economically (Crook 1970, Eisenberg et al. 1972). Aggregation may not be restricted to members of the same species (Gautier-Hion & Gautier 1974, Klein & Klein 1973) and in these cases appears primarily to facilitate feeding in some way. Food distributed differently about the environment has been considered by Crook (1970) and Eisenberg et al. (1972) to cause primate species to adopt different feeding strategies. Thus Eisenberg (loc. cit.) suggests that for species feeding primarily on fruit the best strategy involves the disintegration of a group into small, independently foraging units which communicate the presence of food to each other by loud calls. For leaf-eating species (where food is supposed to be distributed more evenly about the environment) a smaller home range suffices and 'small, cohesive uni-male, social units' are indicated.

Approaches to the study of animal social organisation which have described both the ecological advantages of group living (including the effect this has on individuals' reproductive capabilities), and the means by which this may have evolved, are rarely encountered (but see Barash 1974, Alexander 1974). It seems that to understand the evolution of primate societies one must obtain, in addition to information about the advantages gained by the individual from social life, some idea of the genetical relatedness of individuals in the same and different groups. This is important because the evolution of social behaviour in groups of genetically 'unlike' individuals ('group selection' or 'reciprocal altruism') must occur in quite a different way from the evolution of social behaviour in groups of genetically 'like' individuals ('kin-selection'). Furthermore, closely related individuals are known to behave differently towards each other than they do towards 'non-related' group members (Yamada 1963, Sade 1968, Van Lawick-Goodall 1968).

It may be to the advantage of two distantly-related individuals to behave 'socially' only under certain ecological conditions, whereas it is always to the advantage of two closely-related individuals to help one another. It follows, therefore, that 'family groups' may be inappropriate subjects with which to study the relationship between primate social behaviour and ecology as (with the possible exception of the adult pair) a very precise and close genetic affinity between the group members would be expected to result in a cohesive, affiliative society whatever the ecological conditions. From this line of argument one might expect to find 'family' societies to be correlated with harsh conditions if group-living were an advantage at all in such environments. As no measures of the 'severity' of the environment were obtained in this study, it is not possible to place Indri into this scheme.

Family-living primates, containing individuals bearing equivalent genetic relationships with one another may however be compared in order to examine differences in intra-group social behaviour. Variation in major features of social life within groups of the same size, composition, patterns of reproductive behaviour, diet and ecology, might be expected to reflect phylogenetic differences.

3.2. Social Behaviour in Family-living Primates

Studies in the field lasting from 11-16 months have now been completed on four species of primates which live (probably exclusively) in nuclear 'family' units - an adult pair with their offspring numbering from 1 to a maximum of 3 or 4 In addition to these four species: Hylobates lar (Carpenter 1940, Ellefson 1968, 1974), Symphalangus syndactylus (Chivers 1974), Callicebus moloch (Mason 1966, 1968) and Indri indri (this study), 'family' social organisations are probably present in Aotus trivirgatus (Moynihan 1964), many species of the Callithricidae and perhaps several species of Malagasy lemurs (Petter 1962).

Monogamy has been shown to persist for at least 7 years in gibbons (Chivers pers. comm.), at least 4 years in siamang (Chivers 1974, Chivers et al. 1975) and for at least 3 years in Indri (this study). In all the four species which were subject to long term, intensive studies, territoriality is manifest to a greater degree than for most primates. Early morning loud calls are regularly emitted by all species and encounters with neighbouring groups at territorial borders frequently occur. All species are diurnal and feed mostly on leaves and fruit in the forests they inhabit. Sexual dimorphism is lacking and paternal behaviour well represented by infant transport in _Callicebus_ and _Symphalangus_. All four species defaecate and urinate in the early morning in social elimination sessions. In the larger-bodied family-living species (_Hylobates_, _Symphalangus_ and _Indri_) animals do not reach maturity before 6 years of age and births occur at intervals of 2-3 years. In gibbons, siamang and titis sub-adult males are eventually expelled from the group before forming a mating partnership and acquiring a territory (perhaps near the original group).

Despite similarities in major features of their behaviour, social relations within groups vary considerably. Ellefson (1974) presents little quantitative data and comparisons with _Hylobates lar_ are therefore difficult to make. However, siamang group TS1 (Chivers 1974) had the same composition as _Indri_ Group P in this study: an adult pair and three offspring of different ages. The three offspring accounted for 94% of the play bouts observed in siamang and 86% in _Indri_, a similar result, but siamang spent 12-15% of their daily activity period allogrooming, gibbons 3% and _Indri_ only 0.7% (Group P) or 0.4% (Group V). In siamang and gibbons the frequency with which an individual was involved in allogrooming was a function of its age, but in _Indri_ young animals often groomed each other and adults rarely groomed each other. In Indri and Hylobates dominance in a feeding context was correlated with the frequency of being groomed rather than the frequency of grooming (as in most primates - Sparks 1967) but in siamang the dominant animal groomed most.

Greater differences were found between species in aggressive displacements of one animal by another, than in grooming interactions. In siamang 65% of the observed attacks were by the adult male, 18% by the adult female and 12% by the sub-adult. In Indri most 'attacks' were by the infant/juvenile (33%), adult male (27%) and adult female (24%). Ellefson (1974) does not present comparable data for Hylobates. When the direction of agonistic behaviour is considered, 48% of the attacks observed in siamang were found to be by the adult male on the sub-adult male (the oldest offspring) and 12.7% by the adult female on this same individual. The adult male siamang attacked the adult female four times as frequently as she attacked him. In Indri most 'attacks' were also seen to be by the adult male on the oldest offspring. However the adult female was seen to 'attack' the adult male on 10.3% of all 'attacks' observed whereas the adult male was never aggressive to either the adult female or infant/juvenile. In this sense therefore the siamang adult male was dominant over the adult female whereas in Indri the adult female was dominant over the adult male. In gibbons the data are less clear. Ellefson claims that in one group the adult male was dominant over the adult female whereas in the other study group the two adults had equal status.

The frequency of social interactions also differed considerably in the three species for which there are comparable data. Chivers (1972) estimates that gibbons are involved in social interactions (including territorial behaviour) for an average of 1.7 hours out of 9.5 hours (18%) and siamang for 0.7 hours in 10.5 (7%). In _Indri_ this proportion is about 2% and their daily activity period is much shorter.

During interactions with other groups the males of all four species are active in territorial defence and may engage in fights with neighbouring groups' males. For _Indri_, therefore, inter-group aggression - effected mostly if not entirely by adult males - goes against the intra-group dominance slope, whereas in the hylobatids it runs parallel with it. This major social difference does not appear to be crucial to the structure, ecology and reproductive strategy of the species. These results suggest, therefore, that either 'dominance' is an inadequate concept to explain the structuring of family-living groups or that the identity of the dominant individual (or the presence of such an individual) may be irrelevent to the maintenance of such groups. Furthermore, considerable differences in the frequency and direction of social behaviour appear to have few consequences on major aspects of the species' ecology and reproduction.

3.3. The Adaptiveness of Family-groups

No information was obtained during this study to determine whether small groups of folivorous primates exploited the resources of the rain-forest more economically than larger groups (see Crook 1970, Eisenberg et.al. 1972). It is therefore not possible to discuss any further relationships between Indri social behaviour and ecology. There are however important genetical consequences of group size and composition on individual and social behaviour that have been rarely specified:

(1) In one-male or nuclear family (monogamous) groups the adult males 'know' the identity of their offspring. This is important because it will not be an advantage to a male to invest effort in raising offspring unless those offspring are his own. If it is uncertain whether offspring are his own or not it will be to his advantage to mate with other females (Trivers 1972) or kill the offspring and fertilise the female(s) (Sugiyama 1967). One would thus expect to find paternal care well developed in groups containing one male. Cases of monogamy are rare amongst mammals (compared for example to birds - Lack 1968) because the female plays the physiologically essential role, but where it does occur it seems, as predicted, to be correlated with adult male behavioural investment in the offspring (Orians 1969). Thus in foxes, badgers and viverrids it is associated with donation of prey by males to female(s) and young; in primates it is manifested in transporting the infant (Mitchell 1969). Monogamous reproductive systems are not found in ungulate species (Ewer 1968) and would not, on this argument, be predicted to occur in any grazing, herbivorous mammals. In Indri males do not carry the infant but invest in other ways: by 'allowing' female feeding priority and in taking the active, 'dangerous' role in group defence.

(2) In truly monogamous species little inter-male

competition exists[1] and therefore sexual selection is minimal for most of a male's life. This probably accounts for the sexual monomorphism found in monogamous species (Crook 1972, Alexander 1974) as differences in size, colouration etc. would not have been selected for by inter-male conflict for females (intra-sexual selection) or by female choice of males (inter-sexual selection). There appeared to be no sexual dimorphism in Indri.

Intra-sexual selection may also be responsible for the evolution of aggressive characteristics manifested in 'social hierarchies' and dominance. In monogamous primates, however, this is clearly not the case and dominance, which is related to age and sex, probably has different origins. Thus it may not be important for sex-limited characteristics to be so evident in monogamous societies and situations may arise of female dominance over males (eg. Indri) or male dominance over females (eg. siamang) with little consequence. Dominance, in all likelihood, has more meaning in relationships within than between sexes.

(3) Monogamous societies ensure maximal heterozygosity in the population as each male fertilises only one female. Further analysis of this factor requires information about the distance travelled by mature offspring if and when they are expelled from the groups they were born in, and, consequently the relatedness of mated pairs. Some evidence (Ellefson 1968, Aldrich-Blake & Chivers 1973, Chivers et al. 1975) suggests that offspring do not travel far - a situation which would limit the incidence of exogamy in the population.

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[1] The extraordinary findings of Mason (1966) that Callicebus moloch 'pair-bonded' females mate with other males during inter-group encounters seems to refute this.

The size and structure of populations may have a considerable effect on fitness (Mayr 1963,p655). In particular, a high degree of outbreeding in a population will increase the variety of phenotypes upon which natural selection can act as well as diluting and dispersing local concentrations of deleterious genes arising by mutation. It is for these reasons that future studies on primates threatened by extinction (such as Indri) should concentrate on obtaining information on reproductive behaviour (especially group formation) and population structure.

This thesis has examined the behaviour and ecology of a little-known primate species. The study in Madagascar was a preliminary one and a full understanding of the behaviour of Indri can not be established without observations throughout a reproductive season. Plans for such a study are in progress. Future research should concentrate on the questions originally asked but which failed to be answered viz. how are differences in group size and composition related to individuals' feeding behaviour and food abundance; to what extent are similarities between the ecology and behaviour of primates in Madagascar and Africa/Asia the result of parallel evolution? Questions of interest raised by the study and to which answers could be reasonably obtained are:

(1) To what extent does the behaviour within and between Indri groups change during the period of matings?

(2) Can information concerning the function of behaviour such as loud vocalisations, scent-marking,

social defaecation, territorial defence, be examined by multi-observer or experimental studies in the field?

(3) Is it possible to examine the way in which Indri learn about new parts of the forest - the proximity to neighbouring groups, the location of resources - either by capture/release or purely observational methods?

This study has shown that by observing primates living in small, cohesive groups with a low frequency of social interaction, elements of intra-group communication can be exposed that would have otherwise remained hidden. It has also been demonstrated that all relationships in such groups can be individually examined and, as single members of each age/sex class make up 'family groups', extensive inter-specific comparisons of these relationships can be made.

APPENDIX 1

Specific rules governing observer movement when less than 5 animals were in view.

(i) 4 animals visible.

Case (a): the group of 4 contains the top member of the hierarchy.

Case (b): the group of 4 does not contain the top member of the hierarchy.

In the former case the missing member is ignored and the general rules apply; in the latter the next highest member of the hierarchy is selected and the same principles apply. In the cases described below various hierarchy members are not visible and the animals move up and down the hierarchy whilst always staying in the same relative order. The system thereby constitutes a dynamic animal selection procedure whose flexibility permits the functions described in Chapter 5 .

In case (b) if the dissociated member is seen far away (which is unusual because lateral visibility in the forest was maximally 50 metres and generally about 20 metres) or known to be there by elimination of visible, identified members, a decision had to be made whether moving towards him would jeopardise maintenance of contact with the group as a whole. This was, in practice, rarely a problem as only infrequently would it be certain of the identity of the distant individual, and often he would, in any case, be approaching the rest of the group.

The static group dispersion so far described is an unreal representation. Normally animals are moving about and the situation sporadically (but not continuously) changing. In the following cases, static descriptions will be used to describe movements of the observer (O) and addended where possible animal movements effect an exceptional situation. An asterisk is used to mark the position, if known, of the top member of the hierarchy.

If, therefore, in a 4 + 1* situation the 1* individual returns to the centre of the group, the hierarchy shifts down and O reattaches to 1*. The system is, therefore, reversible. Alternatively, the group may approach 1* in which case O moves with them and reattaches to 1* 'as soon as it is safe'. What constituted 'safe' in such judgement was usually an unambiguous and easily made decision. If there was doubt that 1* was remaining close to the group's centre, O would not follow him.

It was quite possible for O to be situtated within the spread of the group and see nothing. In these cases there was no point in moving as although the probability of locating an animal was high, it was most likely not to be the *individual and it was, in practice easy to move away from the group altogether and thereby lose contact. In any case, searching movements were prohibited for general reasons described in Chapter 5.

(ii) <u>Major group divisions</u>.

Case (c): Group divides into 2 + 3. This often occurred when 2 animals left the other three and was common during group progressions. Often, but not always the other 3 would soon follow them and a cohesive group dispersion recurred.In Case (c), O knows one of three things: that * was in 2, that * was in 3 or that * was in one or the other. In the first two situations O remains close to * and the others(s) individuals(s). In the third 'unknown' situation O remains with the group of 3. If this occurs * may be in 3 (which normally soon became evident) and then Case (c) situation 2 recurs and until * is actually located O remains closest to the next highest member of the hierarchy. If * is not in 3, O still remains with the next highest member of the hierarchy, within this small aggregation.

In any of the three possibilities of Case (c) there could arise a further division, and these constituted the most difficult or complex calculations for the observer:

(i) If O is with 2* (i.e. 2 animals one of which is the top hierarchy member) and 1* splits off, then O remains with 1* only if 3 are not visible <u>or</u> 1* was partnered by the individual who was the SECOND ranking member of the hierarchy that day AND can still be easily seen. If this individual moved further away and 1* does not follow, O likewise, stays with 1* only if the aggregation of 3 can still not be seen. If the partner of 1*, be he any position in the hierarchy, returns to 3 the group is then distributed as 4 + 1* which is case (b) above. The only 'difficult' situation, therefore, is if 1* departs from the rest of the group with the next highest member of that day's hierarchy, when following the small aggregation is preferred to following the larger one.

(ii) If O is with 3* (i.e. 3 animals one of which is known to be the top hierarchy member) and a further division occurs, there are several possibilities. If, for example, 1* departs then O remains with the remaining 2 animals UNLESS 1* has moved towards the rest of the group (2 individuals). Here O is simply staying with 1* and the larger group of animals. Often, however, it was uncertain whether 1* was moving towards the rest of the group, and in these cases O remained with the 2 animals irrespective of their positions in the hierarchy. If one animal, <u>not</u> the highest member of the hierarchy, leaves the aggregation of 3* and goes to the other 2 animals then a situation of 3 + 2* recurs (see case (c) above). If, however, one individual, <u>not</u> the highest member of the hierarchy, moves off in another direction then the split is 2 + 2* + 1.

(iii) <u>Minor group divisions</u>.

Cases such as 2 + 2* + 1, above, are almost always very temporary. O was instructed to remain with any two animals. If a choice arose between groups of 2 animals, O stayed with the group containing the individual of highest relative position in the hierarchy.

(iv) <u>Intermediary cases</u>.

These occurred when the group was essentially together but well dispersed. Usually the adult female and juvenile remained closest to each other whilst the others were separated. The splitting of the group in this way derived most often from a prolonged feeding progression. In a 'ranging' progression i.e. a progression in which the group moves to a distant part of the territory, O is running after the animals trying to stay approximately in the middle or towards the front of the group in the direction of travel. This situation was not conducive to rules or data collection. Most commonly the animals moved from one feeding area to another one by one with occasional and apparently disorganised overtakings. If 1* moved off first then the split was of 4 + 1* and O stayed with 4 until another individual moved towards 1*. O then moved to take up a position between this other individual (x) and 1* where they could both be seen. If they could not both be seen O remained close to x and therefore between 1* and the rest of the group. Further complications may result but as data collection was difficult at these times they do not affect the results beyond biases already discussed.

APPENDIX 2

A stochastic approach to the description and measurement of Indri behaviour.

It was originally considered expeditious to attempt comparisons of gross categories of behaviour between individuals each Circuit. On occasions individual *Indri* were seen relatively infrequently within Circuits and associated with the penalty of sample size reduction caused by extracting records at 15 rather than at 5-minute intervals, this approach made a number of assumptions (see Chapter 2). For this reason the possibility of describing *Indri* behaviour as a two state Markov chain based on the binomial behavioural division of activity into 'feeding' and 'non-feeding' was investigated. Movement, as previously discussed, was difficult to define and other actions were infrequent and widely spaced in time.

The application of stochastic models to behavioural analysis does not represent a novel attitude. It has been the special interest of Cohen (1969, 1971,1972) who has used data from previous primate field studies, and was pioneered by Altmann (1965) who approached the study of social communication of *Macaca mulatta* by computing the relative frequencies of first to fourth 'order' chains through an intermediary measure he called 'uncertainty'. 'Uncertainty' reduced inversely with the order of approximation of the Markov processes examined and permitted a comparison to be made between the 'orders' and the tendencies of certain behaviours or strings of behaviours to precede others. Altmann concluded that out of a possible total of 6.9 bits (binary digits) of information for a species with 120 possible responses, an observed uncertainty of 4.8 bits consisted of 1.9 bits derived from two state (or second order) behavioural combinations. Higher order processes (concerned with the influences of events yet more removed in time) further reduced this figure. Altmann contrived an index of 'stereotypy' from these results.

In this study a similar approach was directed at different ends. Only two activities were considered and an analysis of transition frequencies between these behaviours and themselves required to produce an estimate of the proportion of time spent feeding by an individual that enabled inter-individual comparisons to be made. It was assumed that the behaviour of an individual could be represented by a two-state Markov chain with the transition probability matrix:

$$\begin{Bmatrix} q & 1-q \\ r & 1-r \end{Bmatrix}$$

where q = probability of a Feeding(F) record being followed by a Feeding record, and,

r = probability of a Feeding record being followed by a Non-feeding (NF) record.

p, the probability of a feeding record, is given by:

$$p = \frac{r}{1+r-q} \quad \text{..........} \quad \text{(Laming 1973, page 209)}$$

Population estimates of $r(r^*)$ and $q(q^*)$ and $p(p^*)$ will be approximately unbiased providing that sample sizes for r^* and q^* are large:

$$p^* = \frac{r^*}{1+r^*-q^*}$$

A variance for p^* may then be estimated approximately:

$$\mathrm{Var}(p^*) = \frac{(1-q^*)^2 . \mathrm{Var}(r^*) + r^{*2} . \mathrm{Var}\ (q^*)}{(1 + r^* - q^*)^4}$$

.....(Robinson, pers. comm.)

where for large numbers of transitions F-F and F-NF:

$$\mathrm{Var}(r^*) = \frac{r^*(1-r^*)}{n} \quad \text{and} \quad \mathrm{Var}(q^*) = \frac{q^*(1-q^*)}{n}$$

.....(Robinson, pers. comm.)

In this way a standard error for p^* may be estimated:

$$\mathrm{SE}\ (p^*) = \sqrt{\mathrm{Var}(p^*)}$$

May one assume that the behaviour under study is accurately described by a two state Markov process? For example, may not third or higher order chains of behaviour contain information unrepresented in the simple model suggested above? This possibility was investigated by taking the complete data (see Chapter 2) for the Group V adult male during Circuit VI and counting all the observed triadic transition frequencies: F-F-F, F-F-NF, F-NF-NF, NF-F-F, NF-NF-F, NF-F-NF, F-NF-NF and NF-NF-NF.

Using the nomenclature of Altmann (1965), expected triad frequencies may be defined in terms of the observed dyadic frequencies. This direct method immediately isolates and exposes any loss of information due to differences between second and third order approximations:

For events i, j, k, (in a binary system any two of i,j,k being identical) the expected frequency of the triad i-j-k- is given by

$$E\ (i,j,k) = \frac{N_3\ \bar{p}\ (i,j)\ .\ \bar{p}\ (j,k)}{p(j)}$$

where N_3 is the total number of observed triads and other items represent the observed probability of dyads and monads.

When tested against actual triadic frequencies (Table 2.11) in the sample of data the differences were seen to be non-significant and this supports the contention that second order approximations satisfactorily describe the sampled behaviour.

Estimates of p* differed from actual values in the sample of data by only 2.2% (complete data) and 2.6% (sporadic data). Differences in the clustering of records for different individuals could have influenced the relative numbers of monads, dyads etc. but examination of each individual's records showed that the proportion of feeding did not change according to the numbers of successive records made (X^2 tests = 0.685, 0.298, 0.244, 2.081, 0.334; p ranges from 0.2-0.7).

Finally, from the variance estimates of p*, standard errors of the differences between individuals may be conventionally compared by referring to the distribution of Student's 't'.

TRANSITION TYPE	Expected number	Observed number
F-F-F	33.99	34
F-F-NF	20.96	22
F-NF-F	4.48	6
NF-F-F	19.26	24
NF-NF-F	27.99	25
NF-F-NF	11.88	7
F-NF-NF	30.45	26
NF-NF-NF	190.4	195
TOTAL	339.41	339
$X^2_{(7df)}$	4.3471	
p	0.7 - 0.8	

TABLE 2.11. Observed and expected triad transition frequencies for the binary behavioural category system: 'feeding' (F) and 'non-feeding'(NF). Data contains all records for the Group V adult male during Circuit VI.

APPENDIX 3 (see also Chapter 10)

The "tooth-comb" of Indri and other prosimians

The prosimian primates, with the exception of Daubentonia, possess a small battery of 4 or 6 teeth in the lower jaw which are arranged in the form of a small 'comb' and which are used in grooming behaviour to comb and scrape the fur and skin. The evolution of this "tooth-comb" has been a matter of some controversy (Gregory 1920, Stein 1936, Roberts 1941, Avis 1961). Some authors claim that the dental combination has evolved purely for toiletry and social reasons (Petter 1962, Andrew 1964, Buettner -Janusch and Andrew 1962) but recently this has been questioned with observations of the "tooth-comb" being used for feeding in many species. In Propithecus verreauxi,for example, the "tooth-comb"[1] has been seen to be used in the consumption of fruit (Buettner-Janusch and Andrew 1962), and for prising bark off trees during the dry season (Richard, 1973). Propithecus diadema was observed during the present study to lever bark off trees at Fierenana and subsequently scent-mark the exposed cambium.

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[1] The dental compostion of the "tooth-comb" is itself a controversial topic. Unlike other prosimians the "tooth comb" of the Indriidae contains only 4(rather than a normal 6) teeth. Recently Schwartz (1974) has produced evidence for the 'missing' teeth to be lower incisors rather than canines. The individual tooth-comb may contain therefore one pair of incisors and one pair of canines.

The procumbent "tooth-comb" is used to scrape sap from the surface of lianes and trees in *Galago* and *Microcebus* (Martin. pers. comm.) and a similar dental structure has an identical function in the pigmy marmoset, *Cebuella pygmaea* (Kinsey et al 1975).

Indri probably use the "tooth-comb" more (in time) for feeding than for grooming. During this study the teeth were used as a keen-edged spoon to empty the endosperm of the unripe fruit of *Cryptocarya olseodaphnifolia* and *Tinopsii apiculata*.

APPENDIX 4

Food species list (i) Group P

Group P Rank	Species number	Species name	Vernacular name	% Feeding observations
1	48/50	*Ocotea sp*[1]	Varongy[2]	14.9
2	39	*Ravensara pervillei*	Tavolo lavaravina	13.9
3	44	*Cryptocarya olseodaphnifolia*(1)	Tavolo menalengue	12.5
4	45	*Cryptocarya olseodaphnifolia*(2)	Tavolo radaka	9.6
5	2	*Polyalthia sp*	Amboary	5.3
6	19	*Symphonia sp*[3]	Kijy bonaka	5.2
7	33	*Ficus pyrifolia*	Nonoka	4.3
8	56	*Calophyllum sp*	Vitanona	3.5
9	58	*Tinopsii apiculata*	Voandanary	2.9
10	5	*Edycaryopsis sp*	Amborabe	1.9
11	25	*Ochrocarpus sp*	Kijy fotsy	1.6
12	20	*Symphonia sp*	Kijy ambolava	1.6
13	23	*Symphonia sp*	Kijy	1.6
14	6	*Tambourissa sp*	Amboramalama	1.4
15	28	*Mammea sp*	Mammea bongo	1.4
16	17	*Astrotrichilia sp*	Hetakoaka madinaravina	1.1
17	62	*Garcinia sp*	Vongo	0.8
18	22	Garcinia sp	Kijy bongo	0.7
19	3	*Isolona madagascariensis*	-	0.6
20	42	*Rothmannia sp*	Toalanana	0.6
21	4	*Ficus baroni*	Amoatana	0.5

Group P rank	Species number	Species name	Vernacular name	% Feeding observations
22	40	*Ravensara floribunda*	Tavolomena	0.5
23	7	*Tambourissa sp*	Ambora mainty	0.5
24	46	*Beilschmedia sp*	Tavolosary	0.4
25	38	*Cryptocarya sp*	Tavolo	0.4
26	57	*Cussonia sp*	Voantisi-lanana(1)	0.4
27	60	*Uapaca thouarsii*	Voapaka (beravina)	0.2
28	61	*Uapaca sp*(=*bojeri*?)	Voapaka (madinaravina)	0.2
29	37	*Beilschmedia sp*	Tavaratra	0.1
30	41	*Ravensara helicina*	Tavolonendrina	0.1
31	36	*Beilschmedia opposita*	Sary	0.1
32	47	*Uvaria sp*	Vahimborondreo	0.1
33	30	*Denteromallotus sp*	Minofona koho	0.1
34	26	*Cryptocarya perrieri*	Longotra fotsy	0.1
35	59	*Cussonia sp*	Voantsilana(3)	0.1
36	70	*Tambourissa sp*	Ambora	0.1
37	18	*Allophyllus arborens*	Karambito	0.1
38	52	*Cryptocarya sp*	Vahinana	0.1
39	35	*Cyzygeum sp*	Rotra mena	0.1
			Unidentified:	10.8

[1] Includes *Ocotea cymosa*, *Ocotea racemosa*.

[2] Includes Varongy fotsy, Varongy mainty.

[3] Includes *Symphonia verrucosa* and *Symphonia clusoides*.

APPENDIX 4 (continued)

Food species list (ii) Group V

Group V Rank	Species number	Species name	Vernacular name	% Feeding observations
1	45	Cryptocarya olseodaphnifolia (2)	Tavoloradaka	19.0
2	48/50	Ocotea sp[1]	Varongy[2]	13.1
3	39	Ravensara pervillei	Tavololava-ravina	11.5
4	19	Symphonia sp[3]	Kijy bonaka	7.3
5	44	Cryptocarya olseodaphnifolia(1)	Tarolomena lengue	6.0
6	33	Ficus pyrifolia	Nonoka	3.7
7	25	Ochrocarpus sp	Kijy fotsy	3.6
8	61	Uapaca sp (=bojeri?)	Voapaka (madinaravina)	3.3
9	2	Polyathia sp	Amboavy	3.2
10	62	Garcinia sp	Vongo	1.9
11	20	Symphonia sp	Kijy ambolava	1.6
12	60	Uapaca thonarsii	Voapaka (beravina)	1.5
13	5	Edycaryopsis sp	Amborabe	1.3
14	57	Cussonia sp	Voantsilana(2)	1.3
15	3	Isolona madagascariensis	-	1.2
16	26	Cryptocarya perrieri	Longotra fotsy	1.1
17	23	Symphonia sp	Kijy	1.0
18	24	Symphonia sp	Kijy savondra	1.0
19	56	Calophyllum sp	Vitanona	1.0
20	22	Garcinia sp	Kijy bongo	0.8

Group V Rank	Species number	Species name	Vernacular name	% Feeding observations
21	38	Cryptocarya sp	Tavolo	0.7
22	28	Mammea sp	Mammea bongo	0.6
23	58	Tinopsii apiculata	Voandanary	0.6
24	6	Tambourissa sp	Ambora malama	0.6
25	27	Cryptocarya thouvenuti	Longotra mena	0.4
26	51	Astrotrichilia sp	Vangaty	0.3
27	53	Ocotea sp	Varongy tainjaza	0.3
28	21	Symphonia sp	Kijy beravina	0.3
29	63	Reddhia sp	Voandry	0.2
30	4	Ficus baroni	Amoatana	0.2
31	9	Protorhus thouvenuti	Ditimena(2)	0.1
32	55	Dilobeia thouvenuti	Vivaona	0.1
33	7	Tambourissa sp	Ambora mainty	0.1
34	14	Amcostemum sp	Hazomtoho	0.1
35	32	Ficus sp	Nonoka beravina	0.1
36	70	Tambourissa sp	Ambora	0.1
37	29	Ludia sp	Menarahatra (madiniravina)	0.1
			Unidentified:	10.8

[1] Includes Ocotea cymosa, Ocotea racemosa.

[2] Includes Varongy fotsy, Varongy mainty.

[3] Includes Symphonia verrucosa and Symphonia clysoides.

APPENDIX 4 (continued)

Food species list.

(iii) Other food species consumed by Indri either in very small amounts by the study groups or by other groups.

Species number	Species name	Vernacular name
1	*Tambourissa purpurea*(1)	Ambora mena
71	*Tambourissa purpurea*(2)	-
8	*Protorhus ditimana*	Ditimena(2)
10	*Suregada sp*	Fanambabe
11	*Chrysophyllum boiviniana*	Famelona
12	*Tina dasycarpa*	Famontsilakana
13	*Leptolena bacariena*	Fotoano
15	*Xylopia sp*	Hazoambondvasaraka
16	*Eugenia sp*	Hazompasika
170	*Astrotrichilia sp*	Hetakoak beravina
31	*Syderoxylum sp*	Nato
34	*Canarium madagascariensis*	Ramy
43	*Cryptocarya thouvenuti*	Tavolorano
45A	*Cryptocarya olseodaphnifolia*(3)	-
54	*Sloanea rhodenta*	Voanana/Vanata

APPENDIX 5

The Ecology of Indri Vocalisations.

The characteristics of sounds produced by animals have been subject to selective forces comparable to those acting on morphology and physiology. An animal's sound, if produced for communicative purposes must be adaptive in three ways:

(i) contain information that is not mistaken by the receiver

(ii) possess physical characteristics that are suited to the psychological properties of the receiver, and,

(iii) broadcast information in the correct direction for a suitable distance without loss of information[1].

Marler (1955), in describing the properties of animal sounds best suited for travelling long distances, states that low frequencies are better than high ones. This is because (i) attenuation of sound varies proportionately to frequency (Knudsen 1946, Sivian 1947), and, (ii) low pitched noises will not cast acoustical shadows unless they encounter large objects. This view is correct only if, as is probably the most usual case, attenuation of sound is not required for informative reasons i.e. perception of distance of the sound emitter.

The extent to which animals have adapted their sounds

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[1] Loss of certain properties of the sound by attenuation may, however, be informative in itself.

for distance transmission is uncertain. Altmann (1967) is satisfied that <u>Alouatta</u>, whose roars contain most energy between 200 Hz to 80 Hz are thus adapted. However, other primates living in the dense sound-attenuating medium of tropical rain forest have a wide variety of sound pitches (see below). Relationships between attenuating properties of the environment and the calls of birds living in them has been recently demonstrated by Morton (1970, 1975), and work continues on this subject over short transmission distances, by members of Marler's group in the Rockefeller University (Marten, pers. comm.). Primate loud calls may carry several kilometres, however, and are subject to other attenuating influences. Humidity and temperature are known to affect sound attenuation (Harris 1966), but in the present study these were fairly constant. Rain and wind also played a part in attenuation of <u>Indri</u> calls but their effect may have been mostly due to masking sounds from movement they caused in the vegetation. <u>Indri</u> do not call during heavy rain or on very windy days. Both the topological structure of the environment and the density and form of the vegetation alter the attenuation of sound (Aylor 1972), but the high incidence of non-deciduous plants in the study meant that seasonal variability of attenuation from these factors was low (Embleton 1963, Eyring 1946). The hight at which sound is emitted also affects the transmission distance, not only due to differences in the vegetation at various levels, but also as a result of variation in the temperature and gaseous content of different forest layers (Allen et al. 1972), and the ground's surface characteristics (Aylor 1972).

All these various influences are most important at specific but different frequencies and may result in a very complex source of selection in animal sounds for best distance transmission.

For best sound location by vertebrates with binaural pressure receptor systems, a combination of three types of clues have been proposed:

(i) phase differences between the two receivers (ears),

(ii) intensity differences between the two receivers, and,

(iii) differences in the time of arrival between the two receivers.

Which of these clues animals use under various conditions is a matter of controversy. Phase differences provide ambiguous clues when each ear receives sound more than one wavelength apart. This has often been quoted as limited by wavelengths less than twice the distance between the ears, but in fact must vary according to the direction of the sound. In any case clues from phase differences are limited by the refractory period of the auditory nerve. If this, a probable mammalian constant, is about 1 msec., then frequencies over 1000 Hz are not locatable by this means. Differences in the time of arrival of sound at the two ears provide clues which are probably[1] the same as those from phase differences

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[1] This will depend on sound duration.

(Pye, pers. comm.).

Intensity differences will provide the best clues at high frequencies as these are the ones which are most affected by large objects such as the head.

The most vocal primates emit rather different sounds. Although the loud calls of gibbons have fundamental frequencies similar to those of *Indri*, between 700 and 1000 Hz (Andrew 1963), most of the energy in *Indri* song is concentrated in bands above this pitch. In contrast, almost all the energy in *Cercocebus albigena* 'gobbles' is distributed below 500 Hz (Waser 1975) and *Alouatta palliata* roars vary from 200 Hz to 80 Hz.

Both the information content of the calls and the psychophysical properties of the receiver have so far been omitted from the discussion (see Schleidt 1973). No data are available on *Indri*'s auditory sensitivity. If they differ little from other lemurs then a very broad spectrum of roughly equal sensitivity from 1 kHz to 30 kHz is indicated (Mitchell et al 1970a, 1970b: Stebbins 1971) with a constantly increasing sensitivity between 60 and 1000 Hz. No clear 'best' frequency was found by Mitchell et al. for *Lemur* although this has been shown to exist in some African strepsirhines (Heffner and Masterton 1970). Low frequency sensitivity is probably superior in simian species and high frequency discrimination superior in prosimian species (Masterton et al. 1969).

From purely physical considerations sounds which are low in pitch are most suitable for location by phase differences whereas higher sounds are probably adaptive (i) for auditory sensitivity and (2) for sound location from intensity differences. Adaptations in the structure of primate calls can not be considered only in terms of their transmission properties without a fine knowledge of the calls' information content. The call may only convey one piece of information -'here we are' (Ellefson 1968) - or may be much more informative.

In any case, calls are too variable in structure to indicate strictly definable ecological sources of selection. Marler (1965) states that primate loud calls are purer in terms of narrow bandspread. This may be true of *Presbytis entellus* (Vogel 1973) and of *Indri* and *Hylobates* at one point in time, but can hardly describe the calls of *Symphalangus* or *Alouatta.* Neither are the highest calls structured and the lowest unstructured or vice versa. Information content may be a dominant influence in the evolution of the structure of sounds emitted by primates, and it may also be necessary for sympatric vocal primates to have widely differing calls (Marler 1973).

APPENDIX 6

The Vocal Repertoire of *Indri*.

Indri vocalisations, like those of all lemurs, are essentially discrete (Marler 1965). Two quite distinct calls announce either (a) ground living predators ("HOOT" or 'coup de klaxon', Petter 1962) or (b)aerial predators ("ROAR" or 'aboiements', Petter 1962). Both these calls are loud and carry up to 2000 metres, possibly informing other groups of danger. The roar has been already described (in Chapter 9) as it introduced most *Indri* songs. The roar is produced by all group members simultaneously, lasting from 3 to 10 seconds. It is often preceeded by a hard "COUGH" which was also specifically at response to aerial predators[1]. The hoot is primarily a vocalisation of the adult males and old offspring and may be limited to these individuals. It is emitted in 3 or 4 blasts repeated at short intervals between 2 and 20 times.

A soft BLEAT by infants unable to follow their mother(when transport is refused them at a certain age (see Chapter 10) develops into a louder squabbling WHINE from older individuals when they are displaced by others or otherwise disturbed. Intermediary calls between bleats and whines by individuals of different ages

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[1] Predator specificity in alarm vocalisations 'roar' and 'hoot' may be related to predator position rather than predator identification or habits. On one occasion, before they became habituated, Group IV saw me from the bottom of a valley when I was situated on the ridge top. They looked up and roared. Later that day they moved up the mountain and saw me again when we were at the same level. This time they hooted. The calls may, therefore, provide information on the vertical position of danger rather than its identity.

suggested that these were analogous vocalisations. They and all the other calls described below are soft, intra-group vocalisations.

A series of motivationally connected, quiet disturbance noises were emitted by all individuals, especially when a strange animal was present,and often preceded hoots or roars:

(i) GRUNT: a low, guttural chirp repeated with varying periodicity and intensity according to the degree of disturbance. The sound was too quiet to be recorded on tape but it contained a very high frequency component which seemed to the observer to transmit further than the grunt itself.

(ii) KISS: inhalation through the mouth in a sharp, smacking kiss sound which occurred after a series of 2 to 10 grunts.

(iii) WHEEZE: an inhaled, soft wheeze displayed with a lifting of the muzzle and following a group of grunts and kisses.

Unhabituated _Indri_ perceiving an observer are generally found performing all three vocalisations in the sequence GRUNT - KISS - WHEEZE. Any part of the sequence could be performed, according apparently to the degree of the disturbance, in that order. A wheeze never directly followed a grunt.

Finally a very soft HUM, emitted with closed mouth could be simultaneously produced by several individuals. It appeared to precede a progression or movement which was sometimes only a change of position within a tree.

It's function remains uncertain but the length or intensity of the hum, which could last from 1 to 20 minutes when animals were low in the forest resting, was not directly related to the distance subsequently travelled or, I believe, to the locality visited.

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