THE ECOLOGY AND SOCIAL ORGANISATION OF HANUMAN LANGURS (*Presbytis entellus* Dufresne, 1797) IN KANHA TIGER RESERVE, CENTRAL INDIAN HIGHLANDS.

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ABSTRACT

The ecology and social organisation of Hanuman langurs (*Presbytis entellus* Dufresne, 1797) in Kanha Tiger Reserve, Central Indian Highlands.

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Hanuman langurs were studied for two years between 1980 and 1983 in Kanha Tiger Reserve, Mandla District, a 1945 sq.km tract of hilly, monsoonal, moist deciduous (sal) and dry deciduous forest, interspersed with anthropogenic meadows. Langur population density was 46.15/sq.km., 93% of troops were unimale, 69.6% of males were extra-troop (in bands), troop adult sex ratio was 1:7.9. Both gradual and rapid replacement of troop adult males occurred. An all-male band attacked the study troop, killing three of six infants and, following a phase of consorting, a band male replaced the troop resident male. The observation of infanticide in a low density, undisturbed habitat supports the 'sexual selection' hypothesis and not the 'social pathology' hypothesis. Analysis of intra-specific variation suggests that troop structure and not density is associated with infant killing. The timing of takeovers with respect to the birth season agrees with that predicted if the sexual selection hypothesis is applicable. Activity, feeding and ranging budgets were estimated using scan sampling of the study troop over twelve months. Langurs selected against the use of meadow but for a clump of mixed forest at the centre of their 74.5 ha annual range. Evidence was obtained of territorial site-dependent defence. A dichotomy between troop-troop and troop-band spatial relationships is interpreted in terms of differences in male reproductive strategies and the costs and benefits of conflict. The diet was diverse, including gum and insects, but was dominated by mature leaf and fruit. Trees were not utilized in proportion to their abundance. Range patterns were related to the spatial distribution of highly selected trees and the seasonal consumption of ephemeral food items was related to their availability.

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CHAPTER I

PROJECT ORIGIN, AIMS AND THESIS STRUCTURE

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1.1 PROJECT ORIGIN AND AIMS

This project arose out of a chance visit to Kanha Tiger Reserve in February 1979 whilst travelling from Nepal to Bombay, having had our overland return to England blocked by political events in Afghanistan and Iran. In a brief stay I realised what a fascinating, beautiful and undefiled forest Kanha is: miles of statuesque sal, expansive dadar views, thousands of head of game kept on their toes by abundant tigers. Although a backwater of India, nearby is the land of the Jungle Books, the Gonds of Gondwanaland, the sacred source of the Narmada, the mess where snooker was invented, and the tract where Sleeman eradicated 'thuggee'.

With most of the peninsula a patchwork of paddyfields and villages, such jungle areas as Kanha offer unique opportunities for studying Indian field zoology and botany. The natural history of most of India's large mammals has yet to be investigated in detail. Of the central Indian reserves, such as Melghat, Bandavgarh, Kutru and Simlipal, Kanha was chosen as a study site because of the richness of its fauna, undisturbed forest, abundant langurs, presence of facilities, including a small laboratory, and the welcoming attitude of the staff. This study of Hanuman langurs was prompted by two factors. Firstly, during my brief visit associations between langurs and chital were observed. These, although often mentioned in the shikar and natural history literature, had never been investigated in detail: do they really occur more than expected than by chance, and if so, why? Secondly, the langur infanticide controversy was raging. Much of the evidence put forward in support of and against the competing hypotheses emanated from 'unnatural', human disturbed sites (Curtin & Dolhinow 1978a), different from the habitat in which the species is thought to have evolved. Although one of the first langur studies (Jay 1965) was carried out in a relatively undisturbed moist deciduous forest in Bastar, many of the findings were at variance with subsequent studies (Curtin & Dolhinow 1978a,Hrdy 1977b) and comparatively few hours of observation appeared to have been involved (see Hrdy 1978). Therefore a study of langur social organisation and ecology in remote, undisturbed forest seemed valuable in elucidating the adaptive significance, if any, of infanticide and the unimale-multimale troop structure. Moreover, with the recent blossoming of East African colobine research (Clutton-Brock 1972, Struhsaker 1975, Oates 1974, Marsh 1978) the developments in methodology and approach reported in these studies seemed applicable to an analogous study of the Hanuman.

During this study the direction of research changed. The observation of infanticide diverted effort into related aspects of langur biology. The chital-langur associations, originally the core of the thesis, proved less tractable than expected, owing to the difficulties of watching unhabituated chital; the results will be presented elsewhere. Instead, interest focused on relationships between feeding and ranging ecology. As discussed by Marsh (1981b) investigations of the relationship, if any, between food supply and ranging patterns have been disadvantaged by the complexity of the rainforest environmemt and by incomplete survey of vegetation structure and phenology. With Kanha a simpler, more seasonal habitat, the complete enumeration of trees and the monitoring of the phenology of all tree species, probably increased the chances of detecting such relationships.

The aims of this project were finally clarified as:

1/ Do chital-langur associations occur more frequently than expected by chance ? : if so, what proximate factors are involved and what are the costs and benefits to both species ?

2/ A description of the social structure and patterns of social change for comparison with other populations : what is the adaptive significance of the unimale-multimale distinction ?

3/ Does infanticide occur in undisturbed forest habitats ? If so, why ? Are the circumstances consistent with the "social pathology hypothesis", the "sexual selection" hypothesis, both or neither?

4/ Are langur territorial ? What social "system" mediates the "pattern" of ranges ?

5/ The description of vegetation structure and phenology, activity patterns, ranging patterns and feeding budgets for one langur troop with a view to testing hypotheses integrating these variables. Is the spatial and temporal distribution of food resources related to the pattern of range use ?

1.2 THESIS STRUCTURE.

In the following nine chapters an attempt is made to present the results of observations collected with the above aims in mind. In Chapter 2 the natural history of Kanha Tiger Reserve is described as a background. Similarly, in Chapter 3 the intensive study area is described (with a brief section on a minor study site at Deotalao). Chapter 3 also contains an account of the general methodology used, especially the types and schedule of observations made and the construction of the grid system. In Chapter 4 a brief introduction to pertinent aspects of langur biology is presented. In Chapter 5 the structure and phenology of the forest within the range of the main study langur troop is described; the forest is compared with other Asiatic forests and the influence of man discussed.

In Chapter 6 the main study troop "C" is introduced. The population structure on the meadows is described and compared with other sites. Hypotheses inter-relating some aspects of social structure are reviewed. Reproductive behaviour, particulary birth seasons and birth intervals, are described and observations of mortality and disappearances presented. Changes in the composition of "C" and adjacent troops are described and interpreted. The origin of "C" troop and the killing of "C" infants by extra-troop males is described and the relevance of the latter to hypotheses of the adaptive significance of infanticide discussed.

In Chapter 7 the activity patterns of "C" troop are presented and the methodology of scan sampling discussed. In Chapter 8 the ranging patterns of "C" troop and their overlap with other groups is described. Inter-group relationships are analysed with a view to understanding what behaviours produced the observed over-dispersed pattern of ranges. In Chapter 9 feeding time budgets are given, the selection of species and phytophases are investigated, and gummivory, insectivory and drinking are described. In Chapter 10 the relationship betwen temporal and spatial distribution of food resources and range use is examined and inter-correlations between activity,ranging and feeding patterns explored.

In the Appendices all species of tree and climber recorded from Kanha Tiger Reserve are listed with synonyms and vernacular names. The tree phenology sample is enumerated. The draft of a paper, shortly to be submitted for publication, on infanticide in Kanha langurs, is included and may be useful as an extended summary when reading Chapter 6. Finally, a number of supplementary tables are listed. No final discussion is included: Chapters 6 and 10 review and dicuss diverse aspects of social organisation and ecology respectively.

Tables and figures have been included at the end of the relevant chapters, after the chapter summary. Tables are ordered by letters and figures by numbers. Latin names are given for each species only when first mentioned, except in the case of unusual species. The metric system is used throughout (apart from altitude in Map 6). Some

Hindi terms are used in the text which, although explained when first encountered, are also given here :

'nullah'	: stream
'chattan'	: boulder outcrop, similar to the 'kopje' of Africa.
'maidan'	: meadow.
'sal'	: the tree Shorea robusta
'Baiga'	: a Dravidian forest tribe inhabiting the Kanha region.
'dadar'	: plateau.
'bewar'	: slash and burn cultivation, carried out by the Baiga.

Other abbreviations commonly used are Q for quadrat and "X" for troop identity. Abbreviations for animal age/sex classes are found in Table 4.A. Superscript numbers refer to individual langur identity (e.g. AM^{30} is adult male # 30).

Statistical tests of significance often could not be used, especially with scan data, because of the violation of the assumption of independence of observations (Siegel 1956, Clutton-Brock 1972); those which were used, and descriptive statistics, are listed below with the sources consulted in their computation:

Mann-Witney U	: Campbell (1974), Siegel (1956)
G test	: Sokal & Rohlf (1969)
χ^2 test	: Siegel (1956)
Linear regression	: Campbell (1974), Minitab (Ryan et al 1981)
Spearman rank correlation coefficient	: Sokal & Rohlf (1969), Minitab (Ryan et al 1981)
Multiple regression	: Snedecor & Cochran (1969), Minitab (Ryan et al 1981)
RU	: Rasmussen (1980)

Single-linkage dendrograms : CLUSTAN (Wishart 1982), Sokal & Sneath (1963)

Jacob's preference index : Barnes *et al* (1983), Jacobs (1974)

Shannon-Wiener H' : Pielou (1969)

Dr B.A.C. Don wrote the programme to calculate RU and Dr P. Griffiths assembled the CLUSTAN programme. A 5% ($p<0.05$) level of acceptance is used throughout for statistical tests of significance.

PLATE I

Infant-one No 18 male Hanuman langur of "C" troop. Kanha maidan, Kanha Tiger Reserve. Killed by "Q" band males 19 April 1981 (see Chapter 6)

PLATE 3

The author with "C" troop, Kanha meadows, June 1982. The base of Kuloo chattan is visible in the sal forest behind. (from a transparency courtesy of Belinda Breeden)

PLATE 2

View of the central Kanha meadows and sal forest from a machan (tree hide) at Kuloo chattan, looking SW towards Bija dadar. Kanha village is within sal forest at the extreme right of the picture. "C" troop of langurs ranged to the nullah in the middle foreground (from a transparency).

CHAPTER 2

KANHA TIGER RESERVE

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2.1 TOPOGRAPHY AND GEOLOGY.

Kanha Tiger Reserve is a 1945 sq.km. tract of deciduous forest in the Central Indian Highlands, midway between Bombay and Calcutta. These highlands (the Satpuras) span the peninsular west-east separating the Gangetic Plain from the Deccan plateau (Map 1).

Kanha lies within the Maikal Hills which are situated between the Mahadeo Hills and Chota Nagpur, at 22° 07'-22° 27' N and 80° 20'-81° 03' E. Administratively Kanha falls within Mandla and Balaghat districts of the state of Madhya Pradesh (formerly the Central Provinces) of India (Map 2). Mandla, the district town and Reserve headquarters, is 40 km to the NW on the banks of the Narmada River.

Within the Reserve lies a 940 sq.km. core zone, Kanha National Park, which is under a stricter regime of conservation management than the encompassing forests. The land surrounding the core area within the Reserve forms a 1005 sq.km. buffer zone between the forests and the patchwork of paddyfields and villages beyond (Map 3).

The description of Kanha in this chapter is largely based on Rudman (1912), Schaller (1967), Panwar (n.d.), Mehta (1965) and Brander (1906,1923).

The topography consists of a rugged tangled mass of flat topped hills and ridges enclosing valleys and amphitheatres. Elevation varies from 450 to 950m above m.s.l. with a ridge system running E-W producing spurs which generally project to the north. These hills form the watersheds of the Banjar R. in the west and the Halon and Phen R. in the east which all flow northwards to join the Narmada River. These two drainage systems reflect the division of the Reserve into two hill blocks, largely separated by cultivated plain but joined by the narrow Baisanghat neck. The western block (Maps 3 & 4), made up of the Kanha, Kisli and Mukki Forest Ranges, consists of hills which form a U-shaped amphitheatre, 8km across, drained to the north by the Sulcum R. This large valley contains the the richest game area, the Kanha meadows (with Kanha village at their western edge) and the study sites investigated in this thesis. The eastern block consists of the recently annexed Supkhar and Garhi Ranges.

Geologically, most of the eastern block is covered by the basaltic volcanic overflow of Deccan Trap. However in the western block, the most predominant exposed formations are gneiss and crystalline schists with mica abundant. The hill top plateaux, locally called 'dadars', are capped by laterite often rich in bauxite. The valleys contain black cotton soil in Trap areas and alluvial soils elsewhere.

2.2 PREHISTORY, HISTORY AND ANTHROPOLOGY.

"The greater part of the district is very rugged and mountainous and is still what it has always been to the natives of the other parts of the province, the Ultima Thule of civilization, the dreaded home of the tiger, the Gond and the devil" (Rudman 1912).

The Central Indian Highlands have a very prolonged, obscure, prehistory. While in the Gangetic Plain and the Deccan great empires and civilizations rose and fell, the intervening remote hills and jungles were left in purdah-like seclusion.

In the Maikal hills, isolated by their topography and vegetation, the inhabitants gradually changed from a stone-tool to an iron axe slash and burn/hunter-gatherer culture similar in many ways to an Iron

Age existence. The rate of change of way of life only substantially increased in the last and present centuries with the spreading of Hindu influence and the arrival of state forest administration and exploitation.

Early Palaeolithic artifacts of 20,000 to in excess of 40,000 B.C. are scattered over Middle India. Downstream from Kanha abundant handaxes occur in the Narmada River gravels (Allchin & Allchin 1982). Ghosh (1961) and Mohapatra & Karir (1983) reported on the stratigraphy and lithic industries at Bhamni and Matiyari respectively, in Mandla District. The latter site supported the suggestion (Allchin & Allchin 1982) that the peninsula was more humid than the contemporary environment during periods of the late Pleistocene. The Highlands are also dotted with Mesolithic sites of 8000 - 2500 B.C. yielding microliths and in the sandstone region cave paintings, predominantly of large mammals (Agrawal 1982, Wakankar & Brooks 1976). I found microlith sites scattered over the western region of Kanha, mainly on riverbanks but also on dadars (Newton 1983). The only known cave in western Kanha (Janamala on Chhindi Pathar, Map 4)) did not produce any evidence of prehistoric habitation, though the absence of paintings within the district is probably due more to the non-sandstone geology than the absence of painting peoples. It seems very likely that the descendants of these pre-Aryan hunter gatherers are the tribal peoples of the Highlands today (Wakankar & Brooks 1976), who in the Maikal hills are mainly Baiga and Gond. Kanha is mainly a Baiga area with south Mandla as their stronghold (Elwin 1939). Recently a probable Upper Palaeolithic shrine of 8,000-9,000 BC was discovered at Baghor, 250 km. NE of Kanha (Koenyer <u>et al</u> 1983). This appears to be very similar to those constructed by contemporary Baiga and Kol people, illustrating the considerable continuity and age of the tribal cultures in the region.

The Baiga have been transfused with the material culture of Hindu settlers over the last few centuries but they still remain a very "jungly" tribe with animistic religion, magic and traditions, prolific jungle lore and a tendency for a dark skin, high cheek bones and flat noses. As the Baiga are amongst the oldest inhabitants of India, their origin and affinities are very obscure but they have similarities with the peoples of NE India/Burma and SE Asia (Elwin 1939, Fuchs 1960).

Until it was prohibited in 1868, the Baiga farmed without ploughing (regarded as a mortal sin) using the "bewar" system of slash and burn shifting cultivation. Small patches of forest were felled, burnt and sowed broadcast with cereal and root crops. After at the most three years of farming it would be abandoned and another patch cleared. Fallow "bewar" would revert to grassland and depending on circumstances, to forest successional stages. The Baiga hunted game using spears plus dogs or poisoned arrows. They also set snares and traps, drove tigers from their kills, collected resins, gums, thatch, honey, lac, antlers, fruit, roots, silk cocoons and poisoned fish pools with bark (Elwin 1939,Brander 1906,Pusu pers.comm.). This way of life now continues only in the reserved area of Baiga Chak NE of Kanha. Within the Reserve the Baiga work for the Forest Department mostly in track building and fire protection.

The forests were part of the kingdom of the Garhi-Mandla Gond Rajas from the 12th to the 18th centuries when their state was sacked by the Maharattas (Rudman 1912). In 1818 Mandla was ceded to British India at the close of the Maharatta War. The hills remained a backwater until the 1860's when European forest officers, surveyors and administators made forays into the interior. Captain Forsyth (1889) gives a fascinating account of his exploration of the Halon valley and Brander (1923), once Forest Officer in the Mandla District, describes the game in the Banjar valley (disused name for forest block approximately equivalent to Kisli, Kanha and Mukki ranges) in the early 1900's. In 1879 the forests were gazetted as Reserve Forests by the Forest Department and have enjoyed a firm but variable legal status ever since. The Banjar Valley became famous for hunting, particulary of gaur (B.gaurus), barasingha (C.duvauceli branderi) and tiger (P.tigris) but its inaccessiblity helped prevent over-exploitaion. Bloomfield (1871) despatched the Mad Elephant of Mandla and Hicks (1911) descibes his experiences in the forests and with its maneaters in the 1880's. Maneating panthers (P.pardus) and tigers were quite common with more than 100 people killed by the Sakke maneaters in the early 1900's (Rudman 1912). Best (1935), Hewett (1938), Sterndale (1884), Stebbings (1911) and Aflalo (1935) also describe the region's natural history and their hunting experiences. Kipling set his Jungle Books in the adjoining forests of Seoni and the Wainganga River.

In the Banjar Valley forestry operations began in 1864, producing railway sleepers, and continued intermittently until 1959. Prior to 1931, the Banjar Valley was classified as an ordinary shooting block but in that year, due to concern over wildlife depletion, shooting was confined to a limited class of officers. In 1933, the valley was gazetted a sanctuary, with all shooting except of pigs and birds prohibited and the Divisional Forest Officer was appointed Game Warden. In 1939 the Minister of Forests suggested expansion of the sanctuary into a National Park but this failed due to the expense involved. The area was reclassified as a Game Reserve in 1941 to allow for action to reduce the destruction of regenerating trees by deer. The preservation of high ungulate densities and tree regeneration were seen as incompatible in 1943, resulting in the division of the area into an inner game reserve and an outer shooting block. Due to alarm about the effects an enormous increase in deer numbers was having on tree regeneration, 250 per annum were shot from 1945-1952.

From 1947-51 the Maharajkumar of Vijayanagaram, being permitted to hunt within the valley, shot 30 tigers. However, in 1955 the pendulum swung back and the Banjar Valley Reserved Forest was declared as Kanha National Park. All forestry operations were halted in 1959 and further areas were added in 1962 and 1970, yielding a 447 sq.km. area.

In the east, the Halon valley had a similar history. The Supkhar Sanctuary was gazetted in 1935 but a rapid increase in ungulate and carnivore numbers followed. These came into conflict with cattle and their graziers, resulting in the reduction of the sanctuary area by the administration. In 1942 all the Supkhar area reverted to a district officers' shooting block.

In 1974 Kanha N.P. and its environs became one of the 11 Reserves of Project Tiger, the All-India tiger conservation effort funded by the central and state governments (Mountfort 1981). Concurrently Supkhar and its environs were reinstated as a sanctuary, attached by the Baisanghat corridor to the Park. In 1976, the Suphkar sanctuary was upgraded and merged with the Park yielding a 940 sq.km. core surrounded by 1005 sq.km. of buffer zone. The Park is administered by the Madhya Pradesh Forest Department, under the Chief Wildlife Warden and locally under the charge of the Field Director-Project Tiger with a force of Rangers, Foresters and Forest Guards to manage and patrol the area.

Research within the park began in 1963-65 with Schaller's fieldwork for his monograph on the large mammals (Schaller 1967) and then the short multidisciplinary study in the monsoon of 1972 by a Swiss team (Kurt 1973). Martin (1977) studied the ecology of barasingha, Roonwal & Chhotani (1965) termites, Kankane (1980) langurs and Maheshwari (1963) the flora. Subsequently P.C.Kotwal and R.K.Pandey have investigated the taxonomic and ecological botany (Kotwal n.d., Kotwal & Pandey 1980,1981) and D. Dubey and S. Chandiramani the ecology of chital and gaur respectively.

2.3 CLIMATE AND SEASONAL CYCLE.

In common with the rest of the Indian Peninsular, the Maikal Hills have three seasons:the cold weather (winter), the hot weather (summer) and the monsoon, with extreme fluctuations in temperature and rainfall between them. Fig 2.1 illustrates the climatic regime for the study period recorded by the Forest Department at Kanha village.

The cold weather, from November to February, is cool and moderately dry with very low night temperatures (to -2°C) and meadow frosts during December and January. Fog and dew blanket the meadows in the early morning but by noon the shade temperature is around 30 °C. The forest night minimum is 2-3°C warmer than the meadows. The minor winter rains (only 5-7cm) are produced by the western depressions sweeping across the Highlands. Bird diversity is high at this season, due to an influx of winter visitors; the meadows echo with the bellows of rutting barasingha and the tigers pad the sandy forest tracks to avoid the chilling dew. Towards the end of the winter, in January, the deciduous trees begin leaf fall. Whilst most species remain bare, the near evergreen sal trees in the valleys immediately flush with new foliage.

With an increase in temperature and fall in humidity the hot weather arrives in March. The temperatures continue climbing into May, reaching the high 30's°C by 0900hrs and 42°C by noon. The meadows shrivel, streams cease to flow and the water table plummets leaving dry jungle pools. In the valleys the leafed sal canopies, now flowering, provide welcome shade and reduce dessication of the forest floor. Pronounced game trails are worn into the withered grass enroute to the few water sources and tigers often spend the hot hours with the fish in the jungle pools. The forest floor is carpeted with a thick wadge of brittle dry leaves which thwart quiet progress by man or tiger and invite fire. The hills have a bleak khaki scorched aspect with their skeletal canopies suggestive of a submerged forest but towards the end of the summer the deciduous hill and valley trees flush. The premonsoon showers are heralded by the drifting in from the S.W. of serried ranks of clouds, a fall in maximum temperatures and an increase in humidity.

Short, sharp, afternoon showers with high winds culminate in the monsoon in the third or fourth week of June, often between the eighteenth and twenty-second day. For the first few weeks, the downpours are daily but gradually reduce in frequency and intensity until the rains retreat in September. By October, the monsoon is over leaving landslides, scoured rivers, lush green vegetation and the inhabitants recovering from malaria. The average annual rainfall was 1623mm for 1951-64 (average of Baihar and Supkhar readings, Panwar n.d.) and 1370mm for 1870-1912 at Mandla (Rudman 1912) with approximately 95% falling in the monsoon. The total rainfall at Kanha village for 1980 and 1981 was 1495mm and 1766mm respectively. At the break of the monsoon, termites, snakes, giant millipedes, frogs and a multitude of insects suddenly appear. The withered meadows and the forest floor flush, become waterlogged and within a few weeks the habitat is transformed. Deer congregate in high densities on the meadows to graze and are no longer dependent on isolated drinking sites. In October the river flow subsides and the minimum temperature starts to drop rapidly, affirming the return of the winter.

2.4 VEGETATION

Tropical deciduous forest is the natural vegetation cover of much of the Indian peninsula but in the last 4000 years it has been degraded by man to semi-arid scrub over most of the range (Schaller 1967). The Central Indian Highlands contain many of the remaining natural forests. In Kanha Tiger Reserve there are four main vegetation types - moist deciduous forest, dry deciduous forest, valley meadows and dadar meadows. Here they will be briefly described; Chapter 5 describes a block of sal forest and meadow in detail.

According to Panwar (n.d.) using the classification of Champion and Seth (1968) the following forest types are represented:

Type	3C/C2e:i	Moist peninsular high level sal
	3C/C2e:ii	Moist peninsular low level sal
	3B/C2	Southern Tropical moist deciduous mixed forest
	5A/C3	Southern Tropical dry deciduous mixed forest

Kotwals' (n.d.) ecological classification of habitat types is given in Fig 2.2. Figures 2.3 and 2.4 illustrate vegetation profiles 10m wide on the Kanha meadows (sal forest) and Kodai dadar (mixed forest) respectively. A forest transect, demonstrating altitudinal variation in vegetation type between Kodai dadar and the Kanha valley is given in Fig 2.5. The meadow profile was surveyed in April 1982 and the Kodai dadar profiles in May 1983, following the procedures of Richards (1979). Appendix 1 lists the trees and climbers recorded from the Reserve.

Although there are extensive beds of Tertiary plant fossils in Mandla District (P.C. Kotwal pers. comm.) very little is known about the regions' Pleistocene and more recent vegetation. The fluctuations in aridity detailed in Allchin & Allchin (1982) seem likely to have had a profound effect on the character of the Highlands vegetation.

In the valleys and on the lower hill slopes below 600m the predominant vegetation is moist deciduous or sal forest. The forest is dominated by the 'sal' or 'sarai' tree (Shorea robusta) a Dipterocarp with common associates being Terminalia tomentosa, Syzygium cumini, Butea monosperma and Lagerstroemia parviflora. Sal, covering some 27% of the park area, tends to predominate where it occurs forming 30-80% of all standing trees. A very valuable timber it grows with straight boles to 30m amd 3m girth at breast height. They shed their leaves in February but almost immediately produce leaf flush resulting in a marked fall in nullah water level. Therefore sal forest is nearly evergreen, passing through only a brief period of low leaf density. The forest floor is dominated by Flamengia species of shrub and is quite open, especially in the hot weather, though in the monsoon the shrub patches can reach 2m in height. However, along nullah beds and the lower slopes bamboo becomes the dominant undergrowth forming dense thickets, mainly of Dendrocalmus strictus but occasionally of Bamusa bambors (Panwar n.d.). Scattered through sal forest are rock outcrops or "chattans", similar to the kopjes of Africa, which tend to be vegetated with islands of dry deciduous mixed forest. Trees are festooned with climbers (Bauhinia, Ventilago) and epiphytic orchids (Vanda species).

The sal forest is locally fragmented into a mosaic of grassy meadows ranging from less than a hectare to 6 sq.km, dotted with copses and solitary trees. These meadows (about 21% of the park area) are anthropogenic being the result of Baiga bewar cultivation and village establishment. The further creation of meadows was halted with the prohibition of bewar in 1868. Some meadows were abandoned during the famine of 1874 and others such as Parsatola and Ornakhera abandoned due to disease in the 1930-40's (Pusu.Baiga pers comm.). Kanha F.V. was abandoned at an unknown date but was re-established by the 1940's, probably on Samne maidan (Mehta 1965, Pusu Baiga pers. comm.). A 1906 map (Bodleian D10:24(52)) records 12 deserted and 9 occupied villages within the Mandla District portion of the Park. It therefore appears that the meadows were created by bewar and subsequently repeatedly abandoned and reoccupied as dictated by epidemics and the deterioration of resources such as the soil. Meadows such as Sonph, Rondha, Bisanpura and Sondha (Map 4) have been abandoned in the last fifteen years by relocation of villages to land outside the Park (Panwar 1978).

The Kanha meadows, subjected to very high grazing pressure, have a high species diversity (51 grass species in 6 sq.km.) but low grass height (5-30 cm.) and a large proportion of species are unpalatable to ungulates. In contrast the remaining valley meadows of similar size have lower grazing pressure, lower grass species diversity (25-40 species) and taller grass growth (Kotwal & Pandey 1980).

The meadows remain open due to the stunting and destruction of tree seedlings by ungulate grazing, frost and fire. In December and January the frosts tend to kill the tender sal seedlings on the exposed meadows. With the removal of domestic stock the rapidly increasing wild ungulate populations, particulary chital (A.axis), contribute to maintaining the meadows by browsing saplings. However, the most important factor halting successional change has probably been fire. The meadows have traditionally been burnt during the winter to improve grazing for cattle or to obviate a dire fire hazard in the summer. The Kanha meadows were burnt annually from 1902/3 until 1971 when it was considered that this regime was having a deleterious effect on the fodder of the rapidly dwindling barasingha population (Panwar 1978).

At present, the Kanha meadows are dotted with copses of sal trees and solitaries, especially of Bombax ceiba, Ficus species, Butea monosperma, Zizyphus jujuba and Cassia fistula. The arboreal vegetation reflects both that which was spared during bewar and recent colonization by frost and fire hardy species. The large, mature sals and fig trees are probably relicts and the remaining trees are colonizers. Brander (1906) noted that the copses usually have a large old "nurse" tree standing near the centre with trees decreasing in size and age towards the edge of the clump. The "nurse" tree, old enough to survive independently at bewar, grew to become shelter for emerging trees which enroached radially onto the meadow. The same process occurs at the forest edge, forming a characteristic ecotonal profile of decreasing tree size and age as the forest edge progresses into the grassland. Some meadows such as Kopedubri, once well stocked with barasingha (Rudman 1912), have since been completely enroached by sal forest but elsewhere succession appears to be halted or very slow.

The vegetation astride watercourses is characteristic with the nullah banks and islands typically forested by Mangifera indica, Terminalia arjuna, Ficus glomerata and Syzygium cumini trees. Natural 'bahra' meadows (grass growth >2m in the monsoon) occur on silted nullah beds (Panwar n.d.).

Teak (Tectona grandis), sissoo (Dalbergia sissoo) and khair (Acacia catechu) trees were planted within the Banjar valley during the last century. Of these only teak survives as remnants near Kanha village (Mehta 1965).

Above about 600m on the rocky hill slopes, ridges and dadars the predominant vegetation is mixed or dry deciduous forest, which covers approximately 51% of the Park area. The change, sometimes abrupt, from sal to mixed forest, is related to slope, geology and soils, rather than to altitude per se. The hill forest is scrubby, lower in stature than sal (some 20m high) with a discontinuous canopy but a much greater species diversity; one species rarely dominates a patch. Common species are Anogeissus latifolia, Terminalia species , Gardenia latifolia, Buchanania lanzan, Casearia graveolens, Bauhinia retusa and Sterculia urens (others are listed in Appendix 1). The trees are frequently festooned with climbers particulary Bauhinia valhi and Milletia auriculata. On the slopes the understorey is dense with bamboo, especially in the middle reaches but on the upper slopes, ridges and dadars the ground is clothed with grasses and shrubs. Approximately 41% of the Park area contains bamboo, mostly in mixed forest, but some occurs in the sal-with-bamboo strip between sal-with-Flamengia and mixed forest (see Fig 2.2,2.3,2.4). When the forest canopy is skeletal from February to June the understorey is subjected to the intense heat of the hot weather. However, some of the hill watercourses such as Kerighat and Amahi R. /Mahadeo Gogra waterfall remain moist beneath dense riverine vegetation and a luxuriant understorey of shrubs such as Colebrookia oppositifolia. The hill top plateaux, or dadars, are usually vegetated with meadow and scattered trees, probably as a consequence of the laterite and bauxite sub-surface deposits, inimical to forest growth.

2.5 MAMMALIAN FAUNA

The fauna of the Central Indian Highlands, part of the Oriental zoological realm, is an amalgam of Indo-Chinese, Ethiopean and Palaeartic elements (Roberts 1977,Prater 1971). Very little is known about the autochthonous fauna prior to the Pleistocene but the Narmada River gravels and the Kurnool Caves have yielded an assemblage of that period, similar to the present fauna, of Elephas, Bos, Boselaphas, Cervus, Presbytis, Tragulus, Melursus, Antilope, Tetracerus, Rhinoceros and Equus. This continuity is also emphasised by the sandstone cave paintings of the Highlands rendered by the antecedents of the contemporary tribals

(Wakanker & Brooks 1976). Elephants (E.maximus), gaur, buffalo (B.bubalis), nilgai (B.tragocamelus), blackbuck (A.cervicapra), mongoose (Herpestes sp.), sambar (C.unicolor) and rhinoceros (R.unicornis) appear in Mesolithic paintings (2,500-8,000 BC) and chital, cheetah (A.jubatus), tiger and a langur troop in those of Neolithic/Chalcolithic date (1,000-2,300 BC).

The mammalian fauna of Kanha Tiger Reserve is, for an Oriental area, very diverse and prolific (Table 2.A, see also Schaller 1967, Panwar n.d.). With ten species of ungulate, four of canid and two of large felid, it is more akin to the diversity of Africa than the usual impoverished Asian forests. Such unusual faunal richness is probably due to the presence of the mosaic of meadows within the woodland, which presumably results in higher production being available to terrestial herbivores than in unbroken forest.

The habitat heterogeneity also influences the local distribution of mammals. The blackbuck, an obligate short grass grazer confined to the Kanha meadows (Meier et al 1973), probably reached the valley by 'island hopping' between shifting cultivation through sal forest. The nilgai are confined to the more arid areas of NE Kanha Range such as Silpura maidan. The chowsingha occurs mainly on the dadars and upper mixed forest slopes especially around Bahmnidadar. The sambar, muntjac (M.muntjak) and gaur are found scattered throughout sal and mixed forest, emerging into the open mainly during the nocturnal hours. The chital, the most abundant ungulate, is a deer of sal forest and meadow, rarely climbing higher than 600m into the hills. The hard ground barasingha was once common throughout the sal forests of Central India. The entire population of this subspecies is now confined to the meadows of Kanha, Sonph, Bisanpura and Sondha and the intervening sal forest (Martin 1972, 1973a,b,c, 1977, Panwar 1978). The Kanha meadow population migrates for the monsoon to Sonph where they drop their fawns, a movement probably induced by variation in grass and water availability (Martin 1977).

Sloth bears (M.ursinus) roam the forests, especially in the hills, making nocturnal forays into the meadows to raid termitaria. Wild pigs (S.scrofa) are omnivores of the meadows and sal forests, especially the damper regions. Dhole or wild dogs, fluctuating seemingly erratically in numbers and movement patterns, are pack hunters of ungulates in forest and meadow (Keller 1973). Jackals (C.aureus) are abundant on the Kanha meadows where they are important as predators of ungulate fawns and langurs, as scavengers and in the dispersal of tree seeds. There is apparently a tendency for jackals to be more frequently found in the core and Indian foxes (V. bengalensis) in the buffer zone (pers.obs.).

Tigers and panthers occur at high density (about 0.09 $/km^2$ and 0.05 $/km^2$ respectively) and are commonly seen, especially around the Kanha meadows and Kisli where they are shown to elephant-borne tourists. The remaining large mammals listed in Table 2.A occur at very low density and/or are very rarely seen. In addition, I made a possible sighting of leopard cat (Felis bengalensis) in the monsoon of 1981.

Little is known of the non-mammalian fauna apart from drosophilids (Bachili 1973), termites (Roonwal & Chhotani 1965), a bug-langur association (Newton in press), birds (Guntert & Homberger 1973, Newton et al in prep), and notes in Schaller's (1967) monograph. Disease relationships are discussed in Shah et al (1966) and Mitchell et al (1966a, b).

The wildlife populations of Middle India have declined throughout this century through habitat destruction, hunting and rinderpest epidemics. Elephants and buffalo were seasonal visitors to the Supkhar forests during 1900 (Brander 1923) but the nearest present populations are 560 km and 400 km distant respectively. The cheetah probably became extinct in the Highlands at about the turn of the century (Seshadri 1969), with Brander(1923) only able to report rumours of their existence on the Seoni plateau. The lion (Panthera leo) probably never occured in the hills south of the Narmada R. but even north of the river it was extinct by the mid 19th century (Seshadri 1969). Dunbar Brander recorded on a return visit to the Banjar valley in 1928 :

"In 1900 this tract contained as much game as any tract I ever saw in the best parts of Africa in 1908. I have seen 1,500 head consisting of 11 species in an evenings stroll. It is nothing like that now, but it is probably true to say that it contains more numbers and more species than any other tract of its size in the whole of Asia. " (Brander 1953)

Project Tiger, with its emphasis on species conservation through ecosystem management, has been singularly successful in Kanha. The forests have been rejuvenated with the removal of domestic stock, tiger density has increased and the drastic decline of the barasingha (to 66 remaining in 1970) has been reversed. Management has involved relocation of villages to outside the Park, fire protection, prevention of poaching and the cessation of forest exploitation and cattle grazing.

2.6 : KANHA TIGER RESERVE : SUMMARY.

1/ Kanha Tiger Reserve is a 1945 km^2 forest in the Highlands of Central India, in Mandla District of Madhya Pradesh. The Reserve is a range of flat topped hills and valleys, between 450–950 m altitude, of Deccan Trap, gneiss and schist, which drains into the Narmada River.

2/ Archaeological remains indicate human occupation of the region for some 10,000 years. The descendants of these people are probably the hunter-gatherer shifting-cultivator forest tribals, which in Kanha are predominantely Baiga. From 1879, after British exploration and annexation, the forests were managed by the Forest Department (with tree felling and big game hunting). In 1933 the Reserve area was made into a Sanctuary and in 1955 a National Park with complete wildlife protection. In 1974 it came under the auspices of Project Tiger.

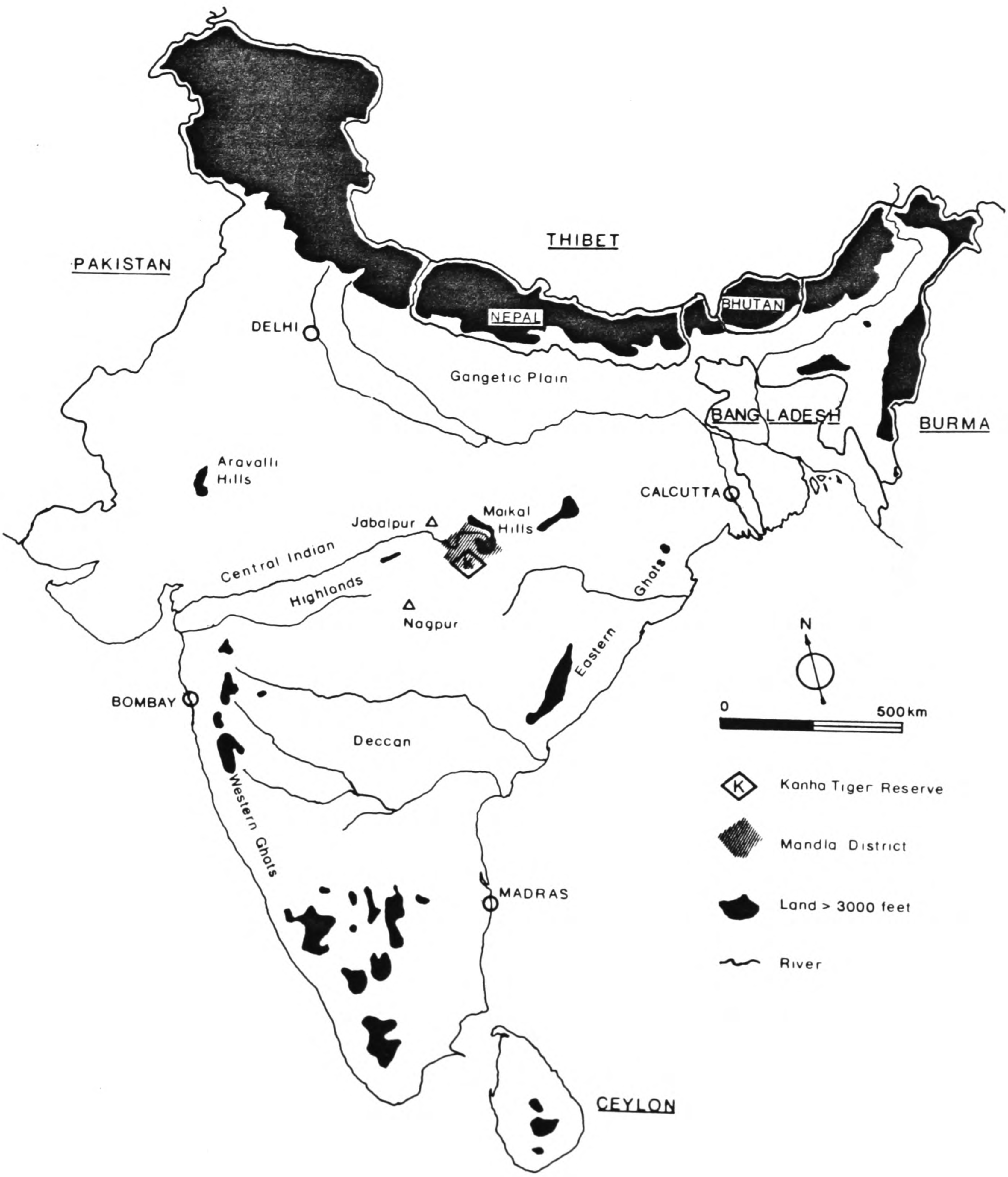
3/ There are three seasons, a cold weather (dry, warm but with night frosts), a hot weather (very dry & hot, to 42°C) and the monsoon (hot, humid, some 1600 mm of rain).

4/ The valleys are vegetated with moist deciduous forest, dominated by sal (*Shorea robusta*), interspersed with anthropogenic meadows. Above some 600 m the hills are covered with dry deciduous forest with bamboo. The plateaux are, owing to superficial geology, mostly open meadow.

5/ The mammalian fauna of the Reserve, with ten species of ungulate, four of canid and two of big cat, is very diverse and abundant. Project Tiger has successfully conserved the Reserve and reversed the decline in many species.

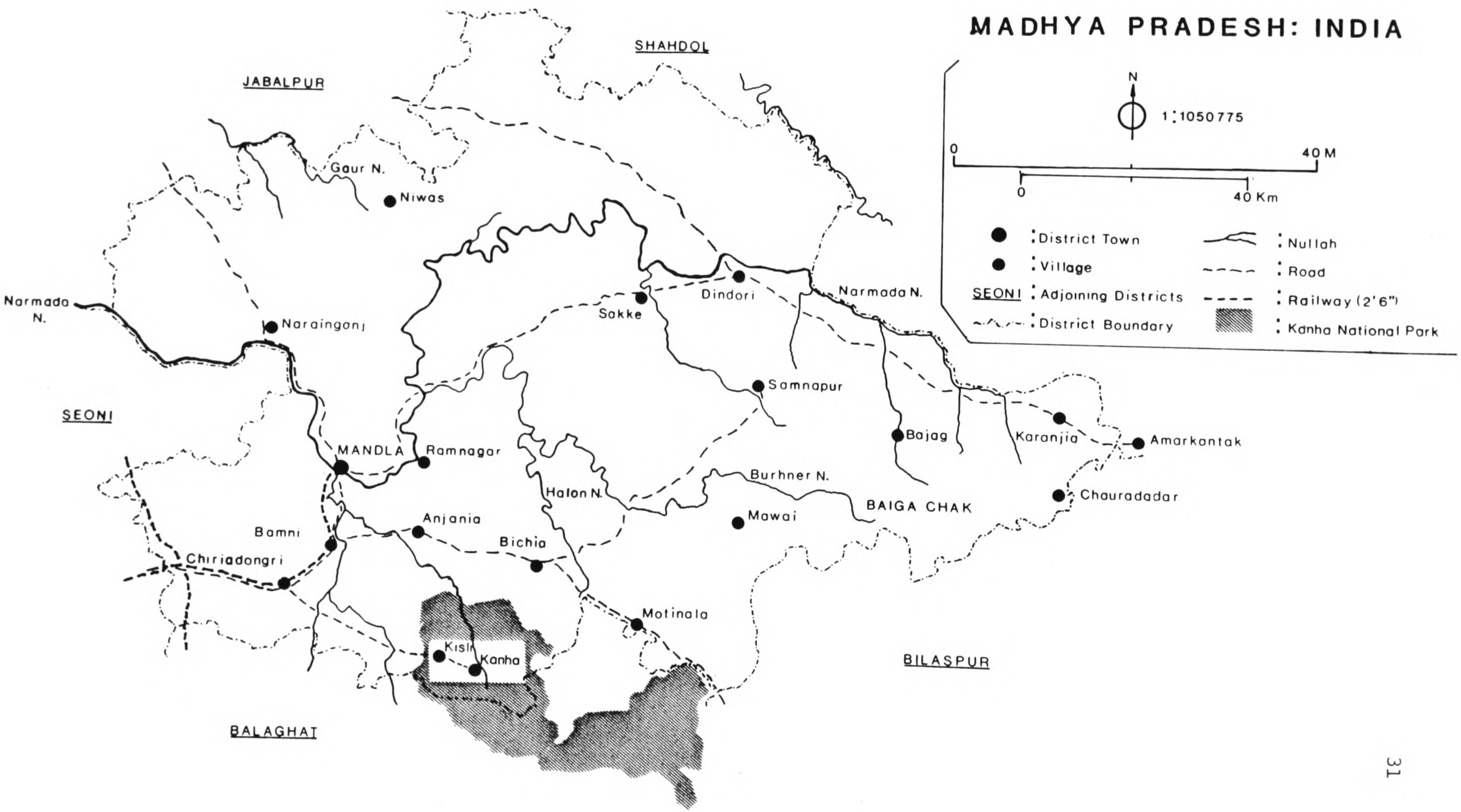
MAP 1 : SOUTH ASIA

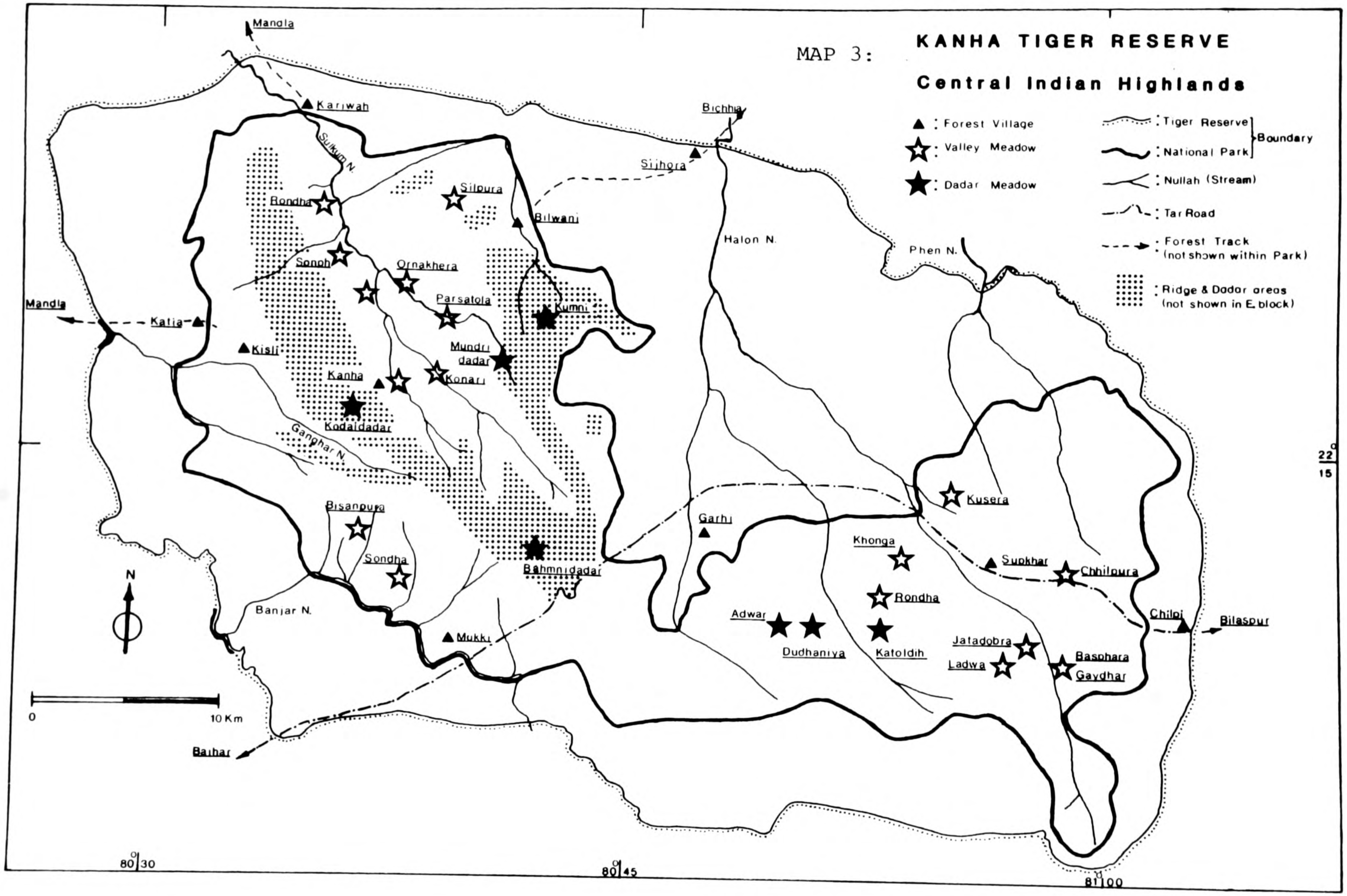
Illustrating the location of
Kanha Tiger Reserve and Highland areas.



MAP 2 : **MANDLA DISTRICT**

MADHYA PRADESH: INDIA




MAP 3:
KANHA TIGER RESERVE
Central Indian Highlands
: Forest Village
: Valley Meadow
: Dadar Meadow
: Tiger Reserve
: National Park
Boundary
: Nullah (Stream)
: Tar Road
: Forest Track (not shown within Park)
: Ridge & Dadar areas (not shown in E. block)
Mandla
Kariwah
Sulkum N.
Bichhia
Sijhora
Bilwani
Silpura
Rondha
Sonph
Ornakhera
Parsatola
Kumni
Mundri dadar
Konari
Kanha
Kodaldadar
Kisli
Katia
Mandla
Ganghar N.
Bisanpura
Sondha
Bahmnidadar
Banjar N.
Mukki
Halon N.
Phen N.
Garhi
Khonga
Rondha
Adwar
Dudhaniya
Katoldih
Kusera
Supkhar
Chhilpura
Chilpi
Bilaspur
Jatadobra
Ladwa
Basphara
Gaydhar
N
0
10 Km
Baihar
80°30
80°45
81°00
22°15

MAP 4: **KANHA NATIONAL PARK**

KISLI, KANHA, MUKKI RANGES

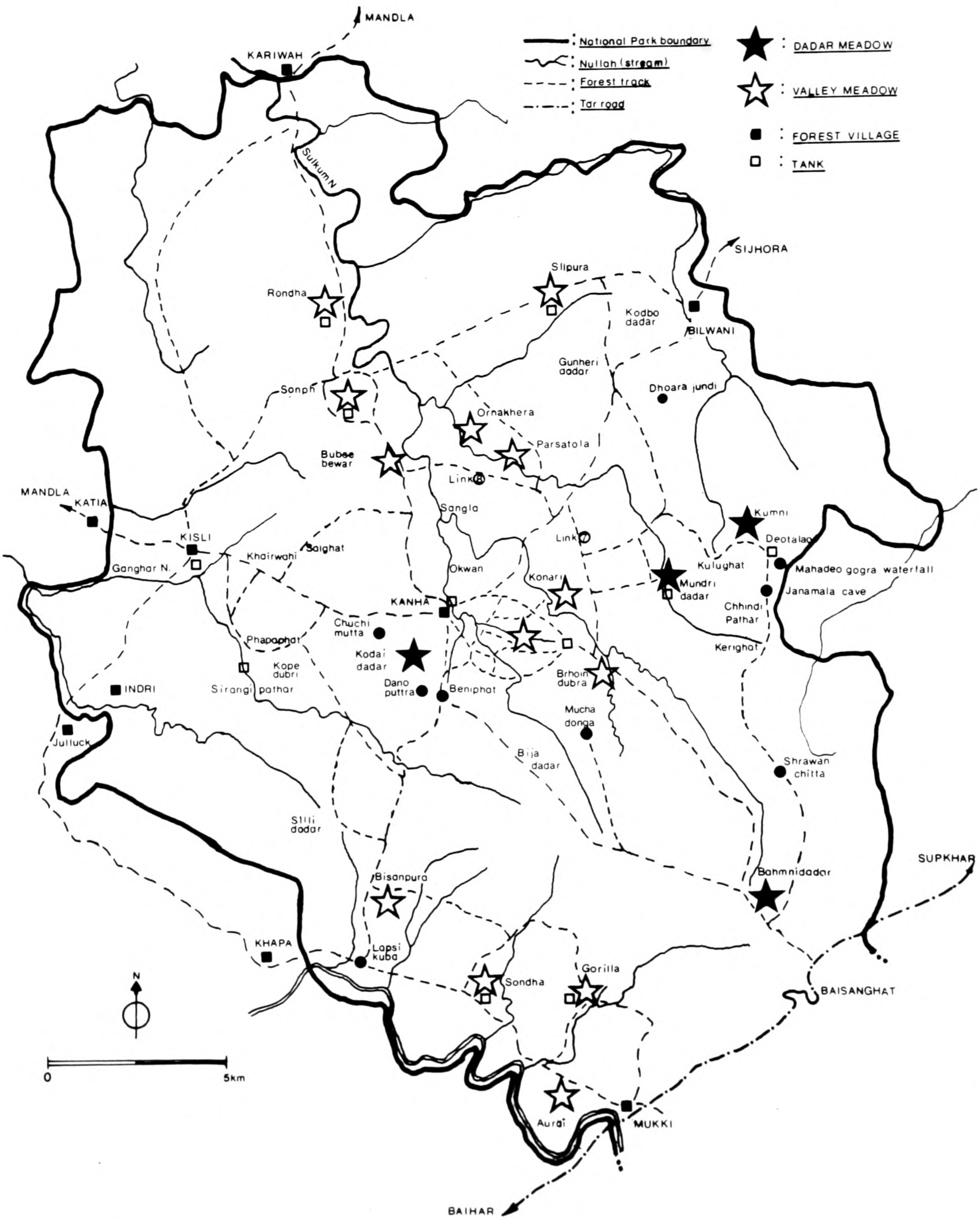


FIG 2.1 TOTAL MONTHLY RAINFALL,MEAN MONTHLY MAXIMUM AND MINIMUM TEMPERATURE AT KANHA FOREST VILLAGE. Data courtesy of Dr. P.C. Kotwal,Madhya Pradesh Forest Department.

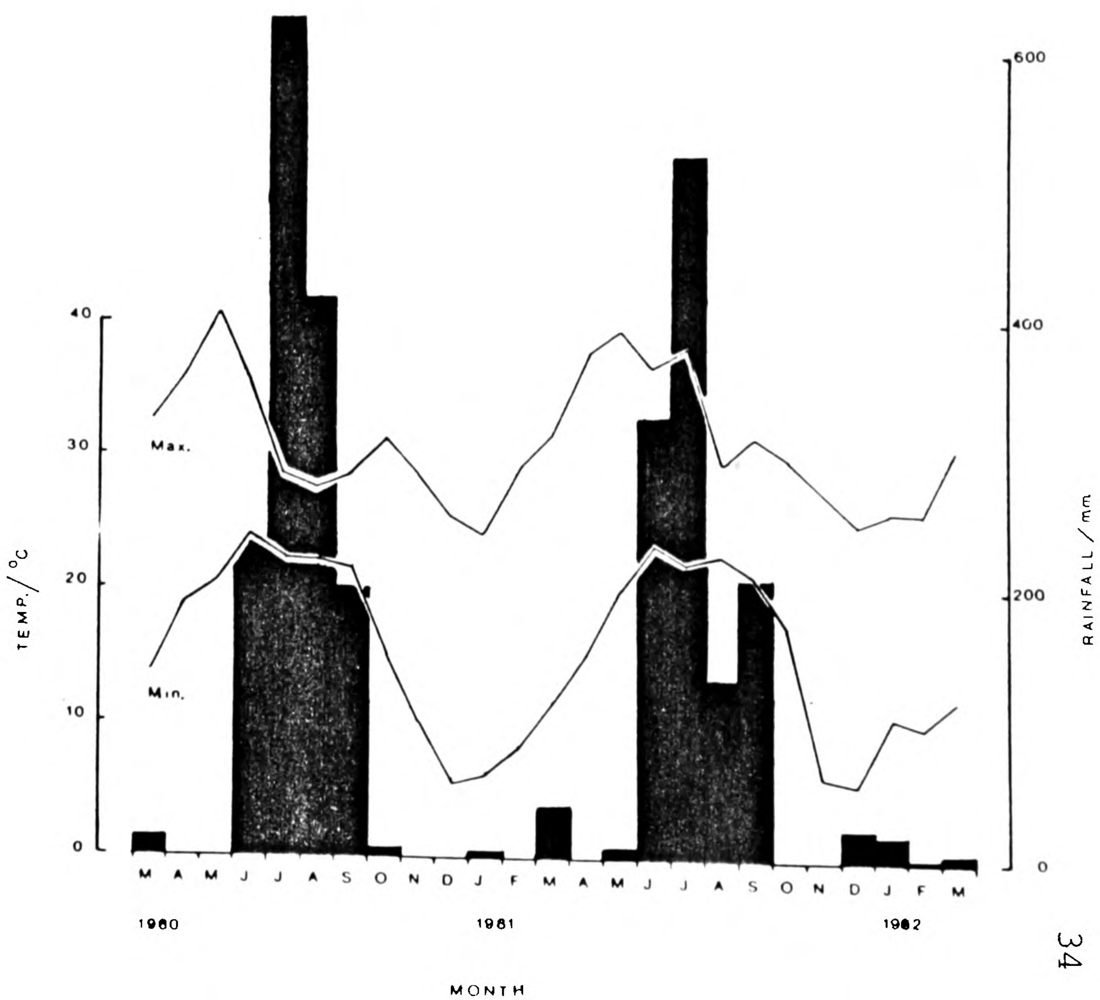
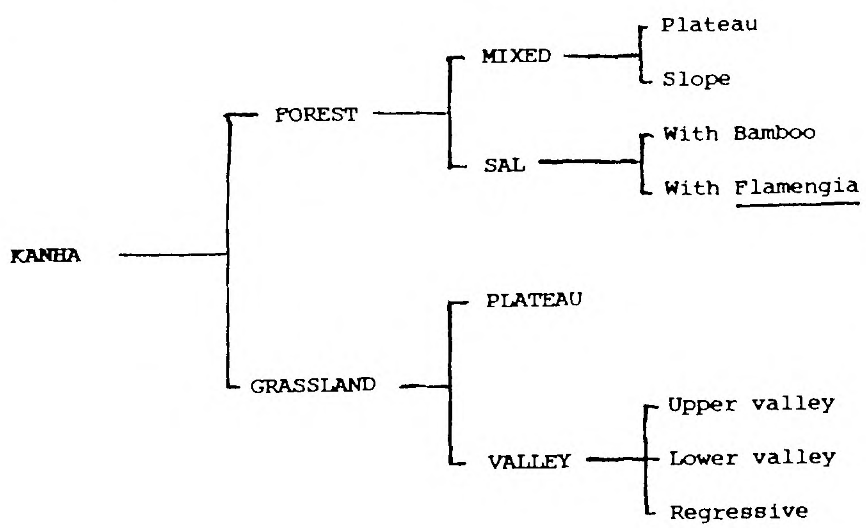


FIG 2.2 VEGETATION TYPES : KANHA TIGER RESERVE
From Kotwal (n.d.)



KEY TO FIG 2.3

10/20, 10/22 : grid coordinates (see Map 6)

Sr : _Shorea robusta_

Ss : _Stereospermum saeveolens_

Bl : _Buchanania lanzan_

Cl : _Cordia latifolia_

Cf : _Cassia fistula_

KEY TO FIG 2.4

Tt : _Terminalia tomentosa_

Ds : _Dendrocalmus strictus_ (bamboo)

Al : _Anogeissus latifolia_

Dm : _Diospyros melanoxylon_

Cf : _Cassia fistula_

Od : _Ougenia dalbergioides_

FIG 2.3/4 VEGETATION PROFILES REPRESENTING 50m X 10m STRIPS OF FOREST.

See opposite for key of symbols.

FIG 2.3 SAL FOREST PROFILE: KANHA MEADOWS. 600m above m.s.l.

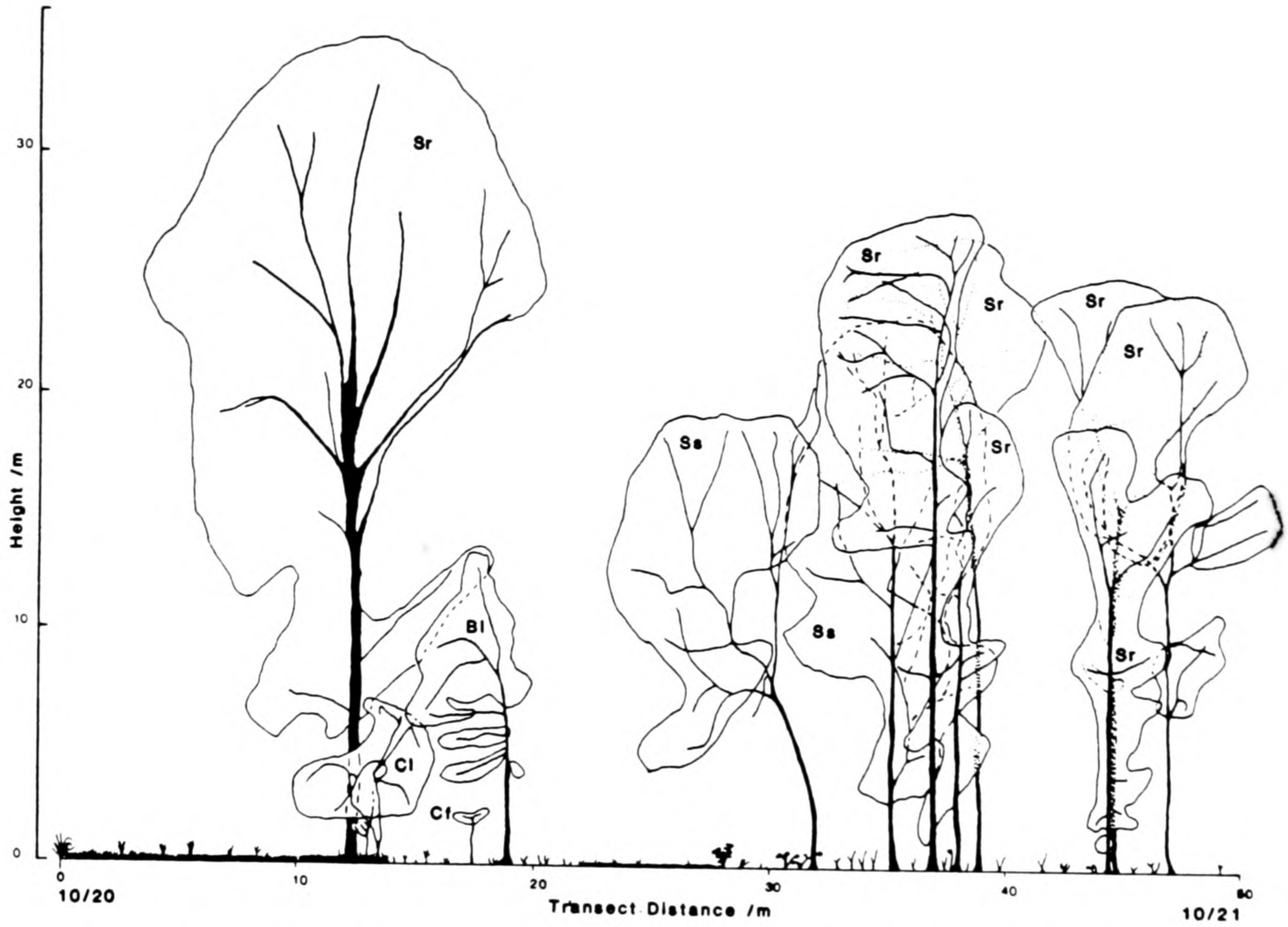


FIG 2.4 MIXED FOREST PROFILE: KODAI DADAR (east slope). 715m above m.s.l.

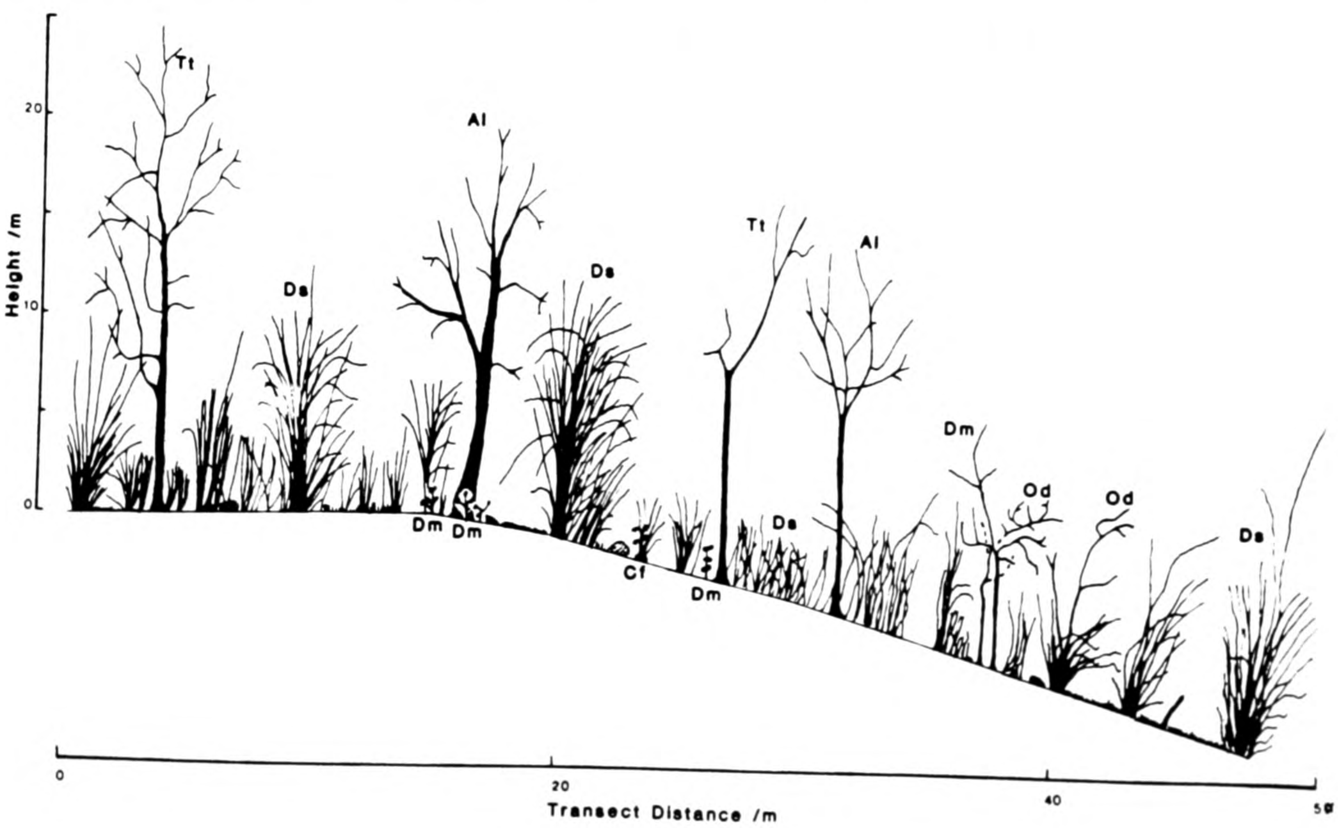


FIG 2.5 VEGETATION TRANSECT 700m X 10m : KODAI DADAR TO KANHA MAIDAN.
Showing the abundance of trees and tree species in 10m sections and the presence/absence of bamboo,grass, *Flamengia semilata* and *Shorea robusta*.

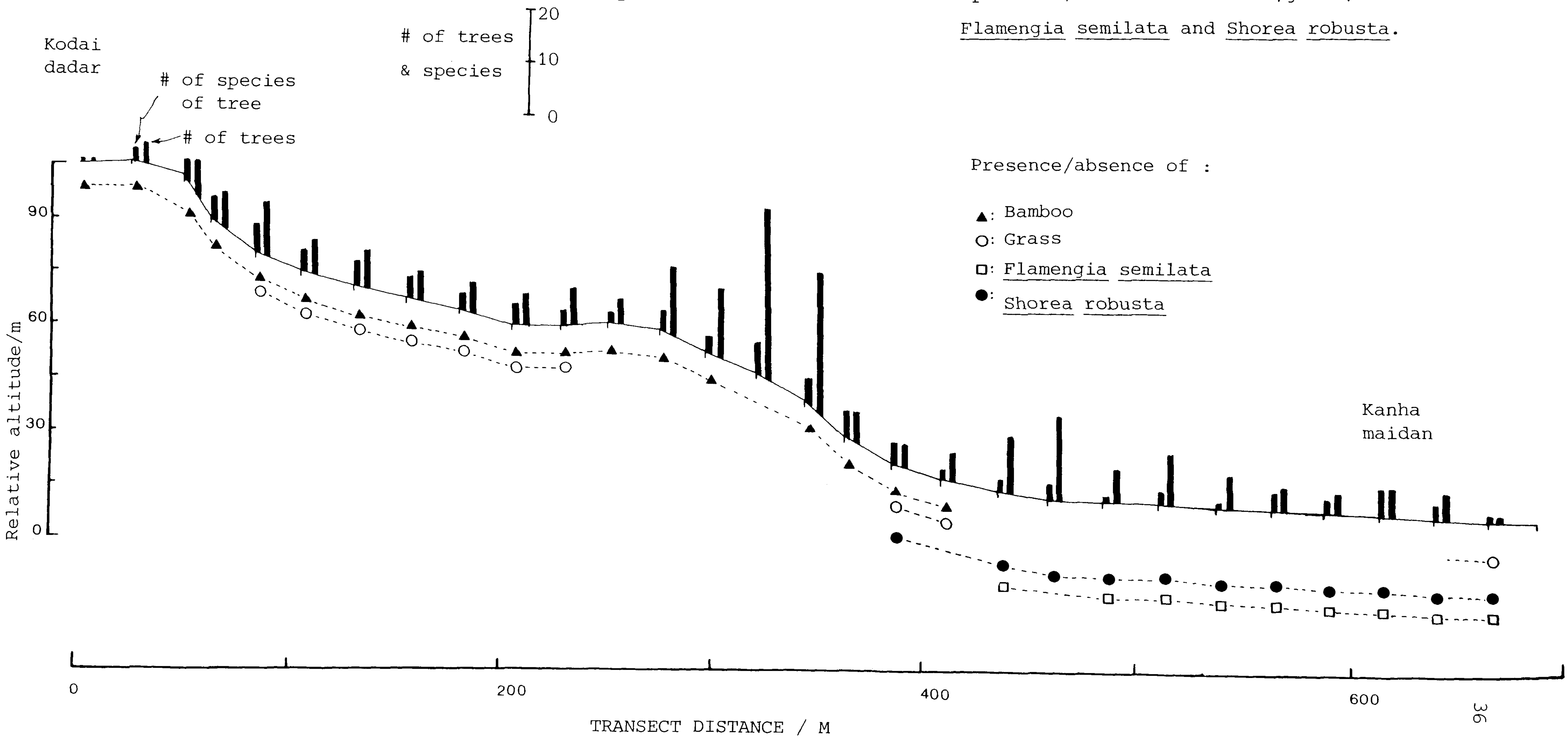


TABLE 2.A

MAMMALS RECORDED FROM KANHA TIGER RESERVE, CENTRAL INDIAN HIGHLANDS.

Sources: Schaller (1967), Claude (1973), Martin (1977), H.S.Panwar (n.d.), P.C.Kotwal (pers.comm.).

* recorded from Kuloo chattan study site, Kanha meadows.

FAMILY Binomial	English name	Vernacular
INSECTIVORA		
Suncus murinus	Grey musk shrew	Chuchunder
Crocidura horsfieldi		
CHIROPTERA		
Cynopterus sphinx	Short-nosed fruit bat	
Hipposideros lankadiva		Mang
Rhinolophus lepidus		
PRIMATES		
Anathana ellioti	Tree shrew	
Presbytis entellus	* Common langur	Langoor
Macaca mulatta	* Rhesus macaque	Lal bandar
PHOLIDOTA		
Manis crassicaudata	Indian pangolin	
LAGOMORPHA		
Lepus nigricollis	* Black naped hare	Karagoosh
RODENTIA		
Funambulus palmarum	* Three-striped palm squirrel	Gilheri
Petaurista petaurista	Common giant flying squirrel	
Mus booduga		
Mus cervicolor		Chooha
Mus platythrix		
Rattus rattus	Black rat	
Rattus blandfordi		
Hystrix indica	* Indian porcupine	Sahi
CARNIVORA		
Melursus ursinus	* Sloth bear	Bhaloo
Lutra perspicillata	Smooth Indian otter	Panikutta
Mellivora capensis	* Ratel, Honey badger	
Viverricula indica	* Small Indian civet	
Canis aureus	* Asiatic jackal	Gidar
Canis lupus	Wolf	
Vulpes bengalensis	Indian fox	Lomli
Cuon alpinus	* Wild dog, Red dog, Dhole	Jungli-kutta
Herpestes edwardsi	* Common mongoose	Newal
Herpestes smithi	* Ruddy mongoose	
Hyena hyena	* Striped hyena	Rela
Felis chaus	* Jungle cat	Jungli-billi
Panthera pardus	* Leopard, panther	Tendua
Panthera tigris	* Tiger	Sher, bagh

TABLE 2.A (Contd.)

FAMILY Binomial		English name	Vernacular
ARTIODACTYLA			
Sus scrofa	*	Wild pig	Jungli-sooar
Tragulus meminna		Mouse deer, chevrotain	Pisura
Axis axis	*	Spotted deer	Cheetal
Cervus duvauceli	*	Swamp deer	Barasingha
Cervus unicolor	*	Sambar	Sambar
Muntiacus muntjak	*	Muntjac, barking deer	Kakar
Antilope cervicapra	*	Blackbuck	Hiran
Tetracerus quadricornis		Four-horned antelope	Chousingha
Boselaphus tragocamelus		Bluebull	Nilgai
Gazella gazella		Indian gazelle	Chinkara
Bos gaurus	*	Bison	Gaur

PLATE 4

An adult female langur of "C" troop on a temitarium in sal forest, October 1981. The tall slender trees at the right of the photograph are Shorea robusta.

PLATE 5

"C" TROOP PROGRESSING NORTHWARDS ACROSS A TREE-LINED NULLAH ON KANHA MAIDAN. OCTOBER 1981

PLATE 6

"C" TROOP ON THE BOULDERS OF KULOO CHATTAN, 23 NOVEMBER 1981, LOOKING SOUTH. AM #30 IS ON THE LEFT.A FEMALE GROOMS AN INFANT IN RIGHT FOREGROUND,THE TREE IN THE RIGHT FOREGROUND IS *Cordia latifolia*.

CHAPTER 3

STUDY AREA AND GENERAL METHODOLOGY

CHAPTER 3 STUDY AREAS AND GENERAL METHODOLOGY.

3.1 STUDY AREAS.

The data presented in this thesis were collected on the central Kanha meadows, supplemented by two days fieldwork at the Deotalao camp. In this section these two areas will be briefly described.

3.1.1 KANHA MEADOWS.

The central Kanha meadows, which form an 8 km^2 area of sparsely wooded grassland within sal forest, lie immediately east of Kanha forest village (see Map 4,5). This location was chosen because :

a/ langurs and chital were abundant and associations between them were frequently observed.

b/ habitat diversity was high.

c/ it was easily accessible from Kanha village.

d/ Khankane (1980) and Lohri and Nagel (1973) had briefly worked on langurs in the same area.

e/ Relatively extensive background information was available on the meadows' vegetation and fauna (Kotwal n.d., Kotwal & Pandey 1980, 1981, Kurt 1973, Martin 1977, Panwar n.d., Schaller 1967)

f/ A large scale map (Martin 1971) was available.

Within the meadows a patch of forest and grassland surrounding a boulder-strewn chattan was chosen as the area for intensive study in April 1980. Situated on the mid-northern edge of the meadows, this area of 0.745 sq.km. lies between Menhar and mid-Desi nullah, Konari maidan, the N.E. meadows and the junction of Circular road and Sijhora track at Kalla puttra. This area was chosen because :

a/ it was occupied by a troop of langurs ("B" troop, see Chapter 6) which appeared likely to be easily habituatable and contained readily recognizable individuals.

b/ it contained chattans which could be used as cover and for quiet movement while watching associations between langurs and unhabituated ungulates.

c/ it was vegetated with a diversity of habitat types (sal forest, meadow and mixed forest on the chattans).

d/ the forest was not used for the baiting of tigers with domestic buffalo (a practice permitted at the start of the fieldwork but abolished in late 1981)

e/ the area had less tourist use than other meadow areas.

The study area, referred to subsequently as Kuloo chattan (named after the central chattan), is contained within Compartment 756 of Kanha Range. The study area boundary was determined by the necessity to include all movements of "B" troop and later "C" troop. The junction of the Sijhora track and Circular "road" was situated at approximately 22° 17' 15" N 80° 38' 3" E (point ★ on Map 5).

The study area of 74. 5 ha contained three major habitat types:

Moist deciduous forest (sal)	51.55 ha (69.2 %)
Meadow, sparsely wooded	20.50 ha (27.5 %)
Dry deciduous forest (mixed)	2.45 ha (3.3 %)

[meadow is defined as those 0.25 ha quadrats which have less than $1m^2$ total tree cross-sectional area at breast height ; dry deciduous forest is defined as the area of the chattans; the remainder is sal forest].

Sal forest dominates the northern area (Map 6,7) consisting of *Shorea* with *Terminalia*, *Syzygium*, *Cordia*, *Diospyros* and *Cassia* abundant. The structure and phenology of the forest is considered in detail in Chapter 5. *Flamengia semilata* and *Holarrhena antidysenterica* are common shrubs, forming dense patches on the forest floor. Saplings of

Shorea, Syzygium and Diospyros occur, though regeneration is slight. Grass cover is meagre beneath the canopy and there is a marked dichotomy in ground vegetation between forest and meadow.

Within this woodland there are three foci of chattans, in the centre (Kuloo chattan), the east and the NNW (Kala chattan) vegetated with mixed forest commonly containing Lannea, Ficus, Anogeissus and Schleichera. The rock outcrops consist of gneiss with quartz inclusions, quartzite and schists. The undergrowth tends to be sparse owing to the boulders but bamboo, Ipomea spp. and herbs such as Blumeopsis foliata (D.Don)Merr., Emilia sondifolia DC., Blumea mollis (D.Don)Merr., Cynoglossum wallichi, Acanthospermum trispidum DC. and Lucas oephalotes were identified.

A tongue of meadow intrudes into the north-west (Samne maidan) and the southern portion of the study area is predominantly meadow. These grasslands are dotted with copses and lone trees of Shorea, Bombax, Butea, Cordia and Lagerstroemia. Of the five grassland associations identified by Martin (1977) on the Kanha meadows three were probably present in the study area:Dimeria connivens, Bothriochloa odorata and Ischaemum indicum associations. Other common species present during Martin's (1977) study were Pseudopagonatherum contortum, Digitaria stricta, Eulalia trispicata and Eragrostis uniloides. Saccharum spontaneum forms dense stands along nullah beds. The dwarf palm Pheonix acaulis is dotted over the meadow, especially in the areas of taller grass. Herbs are not prolific on meadows or within the forest apart from on chattans (see above) but those identified were Polycarpon prostratum (Forssk.)Aschers. ex Schweinf, Rungia pectineta, Evolvulus alsinoides and Plectrocanthus icanus and the orchid Eulophia flava Hook f. The annual cycle of grass standing crop on the meadow, was sampled using 15 0.5m x 0.5m quadrats per month, randomly locatated within the meadow. Mean standing crop (dry weight) was over the twelve months 194.0 g/m^2. Considerably higher grass biomass (max=292.0 g/m^2) was present within the monsoon and winter than in the hot weather (min=117.6 g/m^2). The pattern was due to substantial primary production in the monsoon, probably due to increased rainfall. Kotwal & Pandey (1981) reported a very similar pattern for the same meadows, showing that the mean grass biomass (dry weight) on open grassland was 69g/m^2 but 477g/m^2 in areas from which ungulates had been excluded. Overgrazing and burning were considered by Martin (1977) and Kotwal (n.d.) to have caused a reduction in grass cover and alteration of grass species composition on the Kanha meadows.

The terrain is gently undulating (594m to 621m) and in the west is drained by the Bahera and Menhar nullahs (tributaries of Desi N) and in the east by streams flowing to the Sulcum River. A perennial pond, Menhar bund, is present 50m beyond the western grid boundary. During the hot weather the streams dry up leaving at most 2 or 3 small pools within the tract. The study area is crossed by three forest tracks used by Reserve staff and tourist vehicles. Most foot passage by staff is during the midday hours and is unobtrusive. Occasionally, during the hot weather, elephants were billeted nocturnally within the forest.

The meadows were present 120 years ago (Brander 1906) and were probably created at a considerably earlier date by Baiga bewar (see Chapter 2). Finds of pottery and a loomweight from Bahera N. and of chalcedony and chert microliths and cores from the Desi and Menhar N. confluence indicates prior human occupancy at least 2000 years ago (Newton 1983). Teak (Tectona grandis) was planted in the area in 1880, 1928 and 1954 (Compartment History 1962) and the remnants persist in the NW. The meadow was burnt annually from 1902/3 until 1971 (Panwar n.d.) and two large fires were recorded in 1940 and 1950 (Comp. History 1962). The effect of forestry operations and of Baiga utilization are considered in

Chapter 5.

The large mammals recorded from the study site are indicated in Table 2.A. Those seen daily were barasingha, chital, blackbuck, wild pig, jackal, langur and palm squirrel (F.palmarum), with dhole (C.alpinus), ruddy (H. smithi) and common mongooses (H. edwardsi), jungle cat (F. chaus) and tiger being commonly seen. Sloth bear raided the termitaria on nocturnal forays. Gaur, since the 1976 rinderpest epidemic, only appeared during the monsoon nights. Rhesus macaques (Macaca mulatta) were observed twice during the study on the Kanha meadows on the 28/May/1981 and 1/July/1981. The latter observation was of an adult male. On both occasions chital and langurs gave intense alarm calls. Panwar (pers.comm.) noted this species on Ardwar dadar (Suphkar Range) and Chacko (pers.comm.) saw a solitary animal at the headwaters of Churi nullah (Kisli Range) in 1979. Kotwal (pers. comm.) saw three macaques at Nila nullah (Kanha Range) in 1981 and S. and B. Breeden observed an adult male on 16/7/1983 on the Kanha meadows. Therefore macaques, although common in the surrounding countryside, are rarely encountered in Kanha and apart from the possibilty of Ardwar none are resident within the Park.

3.1.2 DEOTALAO.

In order to investigate langur social organisation in the mixed, dry deciduous, hill forest three days (23-25 April 1981) were spent at the Deotalao patrol camp on Chhindi Pathar in Mukki Range at 22° 17' 30" N 80° 42' 30" E, 10km east of Kanha village. Deotalao is a small lake surrounded by dry deciduous forest close to the Kumni maidan at 823m altitude. Common tree species were:Mallotus phillipensis, Bauhinia vahii, B.retusa, Butea superba, Stereospermum xylocarpum, Acacia pennata, and Dendrocalmus strictus. The undergrowth consisted of Colebrookia oppositifolia, Petalidium barlerioides and Dicliptera veticillata.

Common large mammals present were sambar, wild pig, tiger and sloth bear.

3.2 GENERAL METHODOLOGY.

The approach used in this thesis, in an attempt to answer the questions posed in Chapter 1, derives mainly from the methodology pioneered in East African investigations of colobine ecology. The techniques used with rain forest primates appeared appropriate for use with the leaf monkeys of middle India. In addition they had the potential advantage that interspecific comparisons between primates could be made, in the confidence that variability was a consequence of biology and not confounded by diverse methodology. The studies of Struhsaker (1975), Oates (1974), Waser (1977a), Clutton-Brock (1972), Marsh (1978) and also Altmann & Altmann (1970) and Chivers (1974) were particulary useful for deciding upon the approach.

In this section the schedule of fieldwork and the general methods used for langur observations will be described. Detailed information on methods is given in the introduction to the relevant chapters. As noted in Chapter 1, this thesis does not include the observations collected on langur-chital inter-relationships, which comprised about half the fieldwork. However, as the methods used also yielded information on langur ecology and social organisation, they are briefly described here.

3.2.1. OBSERVATION SCHEDULE.

I was in the field from January to July I980, January 1981 to July 1982 and March to May 1983 ;a total of about 28 months. The first field season was a reconnaissance, to familiarize myself with the Reserve. For the reasons given in 3. 1 the Kanha meadows were chosen as the study area. During this first season the area was mapped, tree identification begun, and a bisexual troop of langurs ("B") studied. After a six month spell in Oxford, rethinking and analysing preliminary results, I returned to Kanha for the major period of fieldwork (18 months). Due to troop social changes (Chapter 6) I switched to observing "C" troop. Unless otherwise indicated, all data presented in this thesis are derived from this major fieldwork season. In the spring of 1983 I returned to Kanha to recensus troops, retake langur 'mugshots' and finish vegetation fieldwork.

A summary of the methods used is given in Table 3.A. Most of the langur and langur with chital data were collected during systematic 'follows' in which I remained in contact with "C" troop from dawn to dusk. Three types of 'follows' were used:

1/ SCAN:the troop was visually scanned at half hour intervals to sample 'instantaneously' langur behaviour and position. This provided information on ranging, activity and feeding (Chapters 7,8,9,).

2/ DROP:the troop was scanned at half hour intervals, as in SCAN, and all green vegetable matter dropped by the langurs during the day was collected. In order to make time for the latter work, a reduced number of variables were recorded during the scans. These 'follows' as well as giving quantitative information on the amount of foliage made available to terrestial herbivores by monkeys, also provided information on langur ranging and feeding.

3/ ASSOC:(=association) the troop was again tracked but at a distance of about 100m and watched from concealment (in trees, behind rocks) so as to be able to observe the movements of unhabituated chital in relation to langurs. These 'follows' also yielded information on langur ranging, feeding and social change.

These three types of 'follow' were concentrated during the second half of the month in a regular order (see below), interspersed with the monitoring of tree and gum phenology, and terminated with the sampling of meadow grass standing crop.

Arrangement of scheduled observation time "C" troop:

Observation	A	A	A	A	A	D	d	D	d	T	T	S	S	S	S	S	G
Date of month	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31

Key

A : ASSOCiation follow

D : DROP follow

d : sorting vegetation collected during D

T : tree phenology recording

S : SCAN follow

G : grass standing crop sampling

During all fieldwork in the study area "C" was monitored ad-lib for social change and other events of interest. Tree enumeration, population survey and observation of chital-langur associations at mohwa (Madhuca indica) trees was done outside the monthly observation bouts. The first half of each month was spent doing the latter fieldwork projects, bringing in supplies, doing paperwork and exploring other reserve areas.

The monthly langur 'follows' and associated monitoring was carried out from February 1981 until March 1982 but February and March 1981 have been excluded from the analysis owing to dubious reliability. The schedule of systematic fieldwork followed the above pattern with two exceptions (the mean shift in date of each follow was 1 day with a maximum deviation of +3 days). In June 1981 only one DROP follow was carried out but an additional SCAN follow substituted. In September 1981 the observation was unavoidably halved to 6 days (5 x SCAN + 1 x DROP) due to illness.

The number of hours per month of scheduled observation is shown in Fig 3.1 and Fig 3.2 illustrates variation in daylength and the length of the fieldwork day.

Total langur contact hours for 1981/1982 were:

ASSOC	follows	695 hours	
DROP	follows	301 hours	1853 hours
SCAN	follows	857 hours	
AD-LIB		300 hours	
TOTAL		2155 hours	

3.2.2. GRID SYSTEM.

For the analysis of ranging patterns, vegetation distribution and for the description of the location of events a spatial frame of reference was required. The initial method, plane table mapping, was abandoned in favour of surveying in a grid system on the ground. A grid of 298 quadrats, each 50m X 50m, was constructed (total gridded area = 74.5 Ha) using 6/10 to 12/10 (x / y cordinates, see Map 6) as a baseline. Initially an area of circa 800m x 800m was gridded, centred on Kuloo chattan, as this area was thought to encompass the range of "B" troop. Whenever "B" and, in 1981/82, "C" went beyond the grid it was extended as soon as possible. The grid was surveyed in by taking right-angle offsets at 50m intervals from the baseline. Using a tapemeasure and two straight sighting bamboo poles these offsets were continued as parallel lines 50m apart through the forest and bamboo pegs erected at 50m intervals. The distance between parallel lines was frequently checked for distortions. Nevertheless, cummulative errors probably caused a decrease in accuracy towards the periphery of the gridded area. However, measurement of a random selection of 16 distances between adjacent grid pegs gave a mean of 50.24 ± s.d. 1.32m (a mean error of 0.48 %). Variation in relief was small (some 27m) and therefore errors from this source would be minimal. Though the most pragmatic, this method was difficult and time consuming to use in dense forest, with Kuloo chattan necessitating 'dog legs' which initially produced distortions. However, the level of accuracy was well within the accuracy of the recording of langur position.

The bamboo pegs were susceptible to termite attack and uprooting by elephants and langurs. They therefore had to be replaced three or four times during the study. The gridded area was mapped with reference to the pegs, at 1:2500 and fieldmaps were ammonia printed at 1:5000.

For watching unhabituated chital rapid and quiet observer movement was necessary and therefore in the forest area lanes one foot wide were swept clear of the thick layer of fallen leaves between grid pegs (giving 3-4 km of quiet routes). This activity was carried out prior to the ASSOC 'follows', finishing at least 2-3 days before observations began in order to avoid the effects of disturbance. Such clearing was unnecessary in the monsoon due to the dampening of the leaves. The grid cells were not labelled on the ground but were easily identified (using the SW corner) by referring to the annonotated fieldmaps.

3.2.3. HABITUATION AND LOGISTICS.

Although generally disturbed by the approach of humans, "C" troop became habituated within two months to the author's presence at 1-10m. This habituation, and the fact that langurs were readily distinquished as individuals, obviated the necessity for provisioning, marking or indeed any physical contact with the study troop. A neutral relationship between langurs and observer was maintained. A 'zig-zag' route was used when approaching the troop in order to avoid the alarm caused by a 'head-on' course. My presence appeared to have very little influence on "C" though particular care had to be taken during encounters, especially those involving infanticide, to avoid affecting the outcome.

I wore the same clothes every day to aid habituation and the equipment used depended on the season. In the hot weather 4 litres of drinking water had to taken to the field daily, whilst in the monsoon notes were taken with hands and paper inside a large plastic bag shielded by an umbrella mounted on a walking stick. "C" had to be habituated to the umbrella and great care had to be taken to open and close it very slowly or the troop showed considerable consternation!

For 'follows' I left at first light, having ascertained the troop's sleeping site the previous evening, and returned after sunset. The study area was a 20-30 minute walk from Kanha village. With a few exceptions the fieldwork was carried out alone. Mungal and Mohan Baiga assisted in the collection of dropped vegetation for part of DROP follows (only in those situations were langurs >100m from the dropped vegetation), maintained the grid pegs, swept the inter-peg lanes, assisted in tree enumeration, phenology monitoring and the cutting of grass stand crop samples.

All observation was done with the unaided eye or Hartmann 10 x 50 binoculars which proved excellent apart from being chronically ravaged by fungus in the monsoon. All data was duplicated using carbon paper or rewritten and sent back to Oxford at 3-monthly intervals.

3.3 STUDY AREA AND GENERAL METHODOLOGY : SUMMARY.

1/ A 74.5 ha tract of Compartment 756 of Kanha Range at the edge of the central Kanha maidan was chosen as an intensive study area. It consisted of 69.2 % sal forest, 27.5 % meadow and 3.3 % mixed forest (on isolated rocky outcrops). The meadows were created, prior to 1868, by Baiga slash-and-burn cultivation and now support high carnivore and ungulate density.

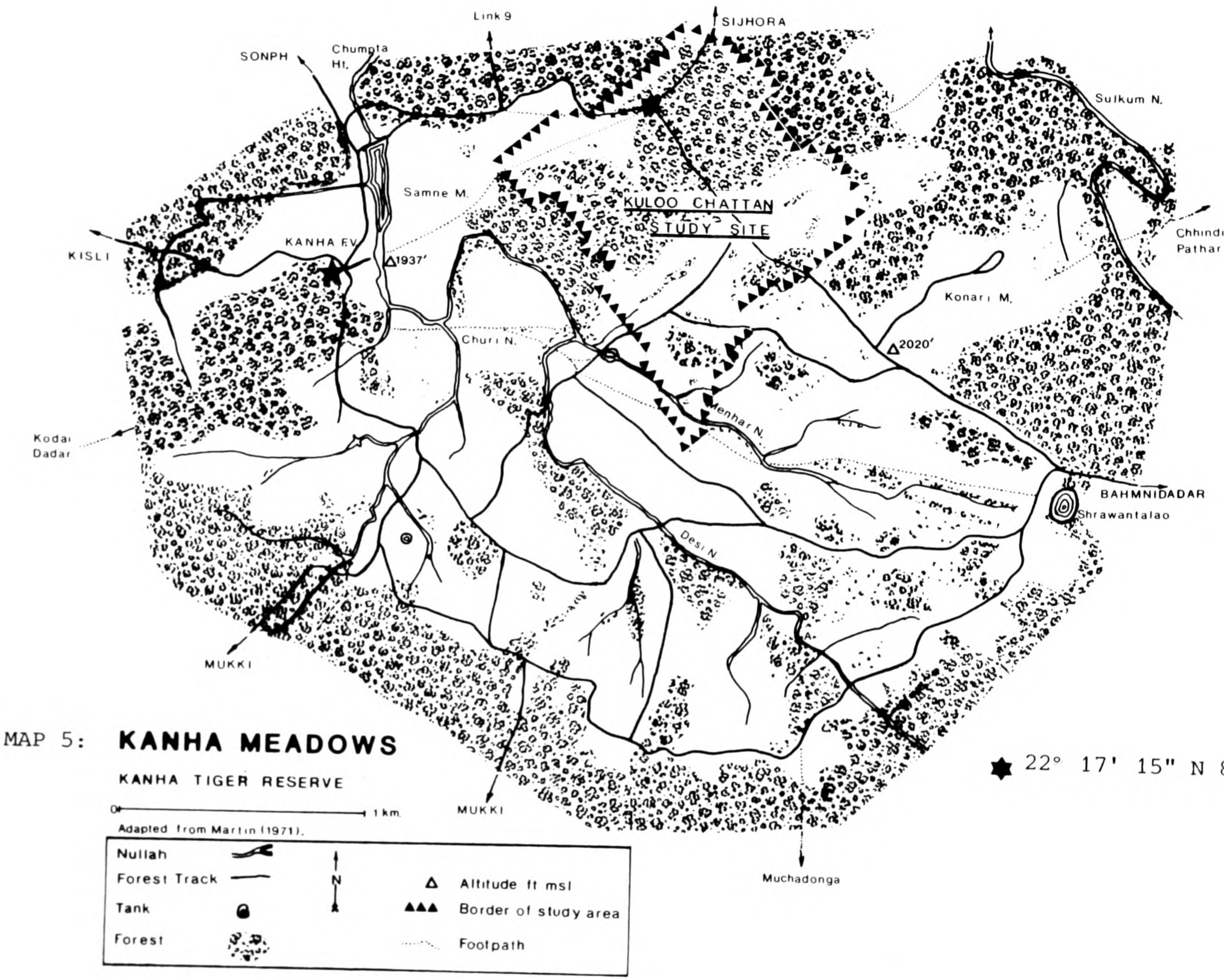
2/ Deotalao, in the mixed forest of Chhindi Pathar, 10 km^2 east of the meadows was chosen as a minor study area.

3/ Of 28 months fieldwork (2155 langur contact hours), between January 1980 and May 1983, data collected between April 1981 and March 1982 is used in this thesis. One troop, "C", was followed from dawn to dusk on 12 days in the second half of the month, for 12 contiguous months. On five days "C" was scanned at half hour intervals to sample 'instantaneously' individual langur states of ranging, feeding and activity. On a further five days chital-langur relationships were recorded, also yielding information on langur ranging and feeding. On another two days all vegetation dropped by the troop was measured and the troop scanned at half hourly intervals. "C" was also opportunistically watched during the first half of the month and monitored for social changes.

4/ Tree and gum phenology was monitored monthly.

5/ The study area was mapped and gridded into 298 0.25 km^2 quadrats, demarcated on the ground by bamboo stakes.

6/ "C" troop habituated easily, allowing my approach within 10 m and a neutral relationship was maintained. They were never provisioned, marked or interfered with in any way.



MAP 5: **KANHA MEADOWS**

22° 17' 15" N 80° 38' 3" E

FIG 3.1 SYSTEMATIC OBSERVATION TIME.
Number of contact hours per month
with "C" troop.

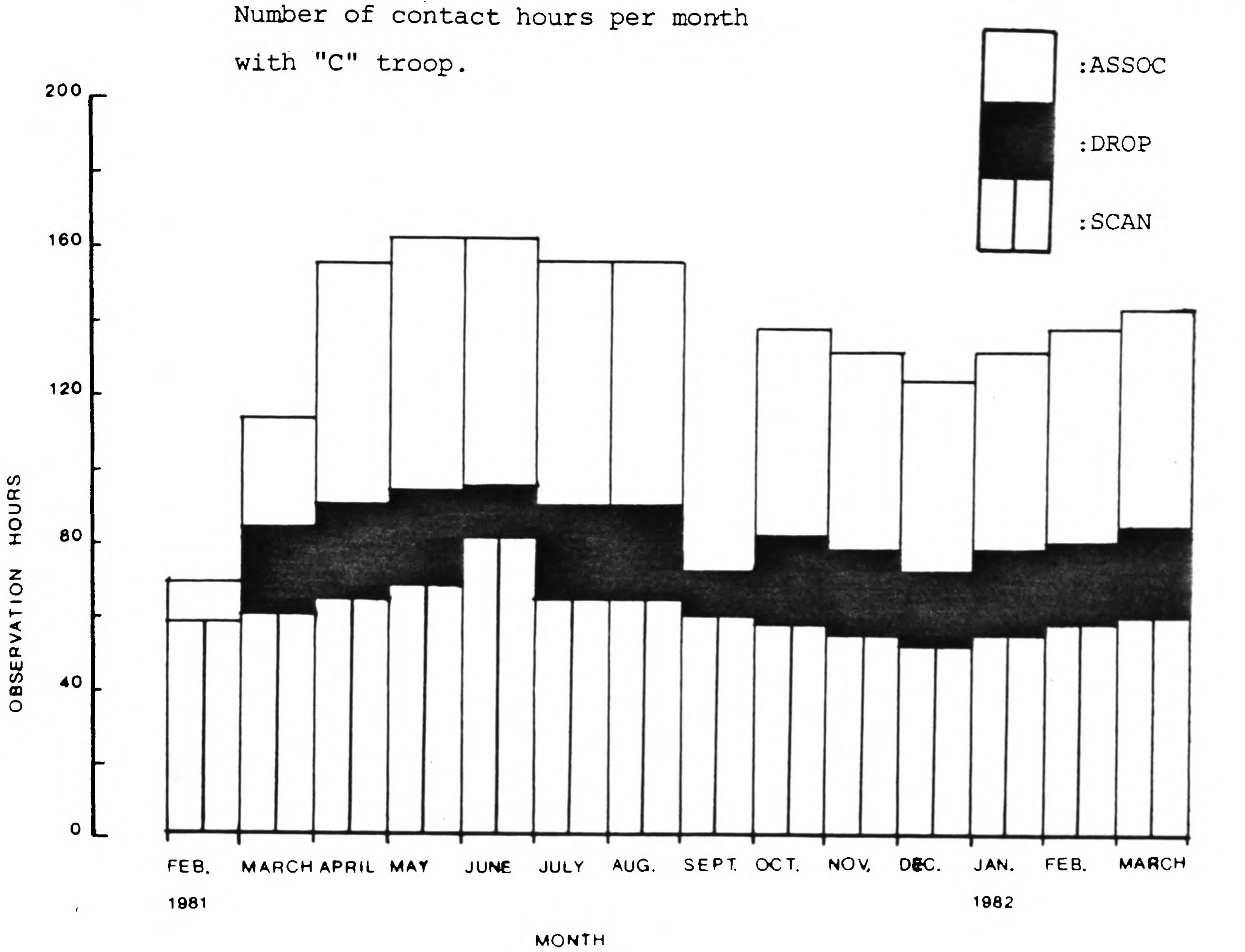
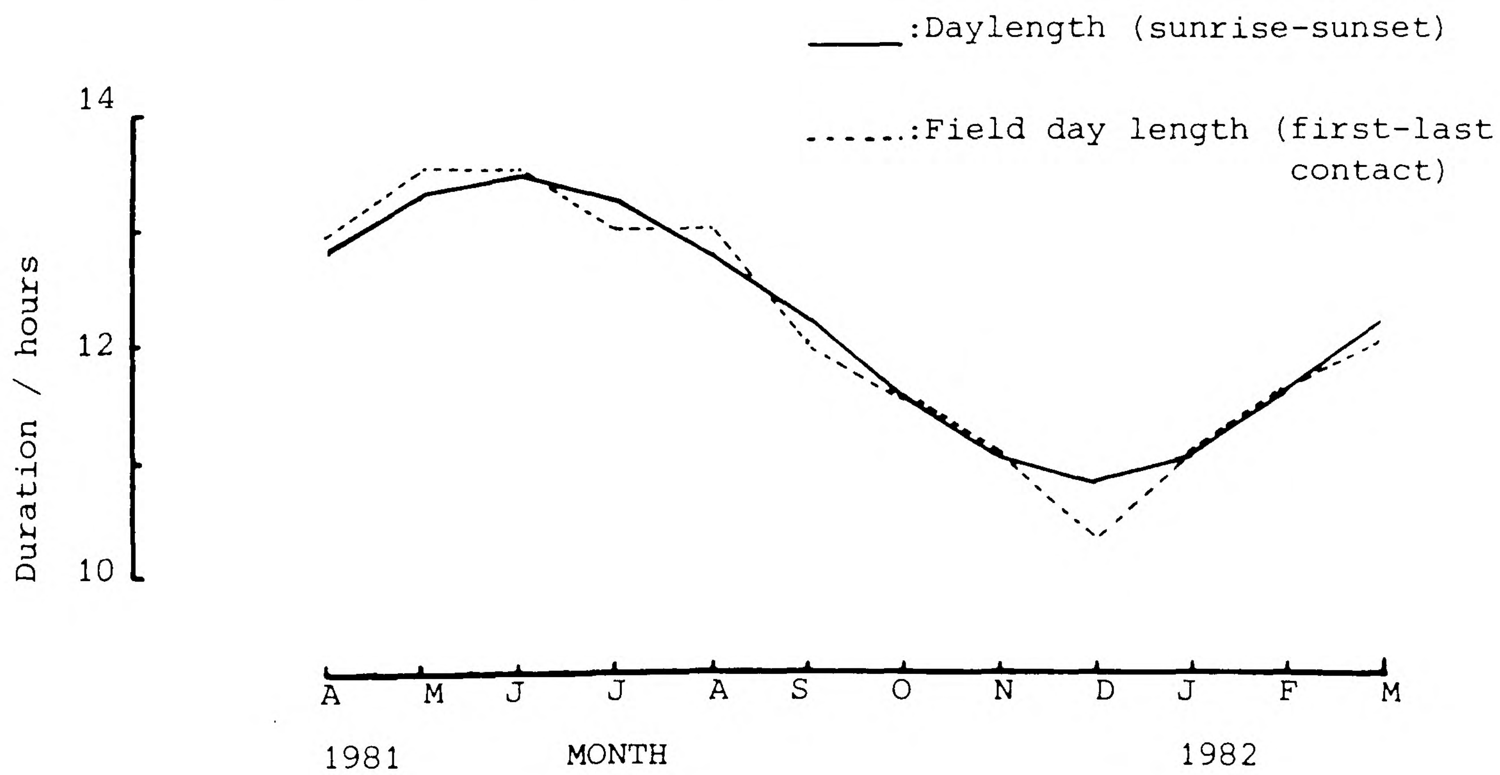
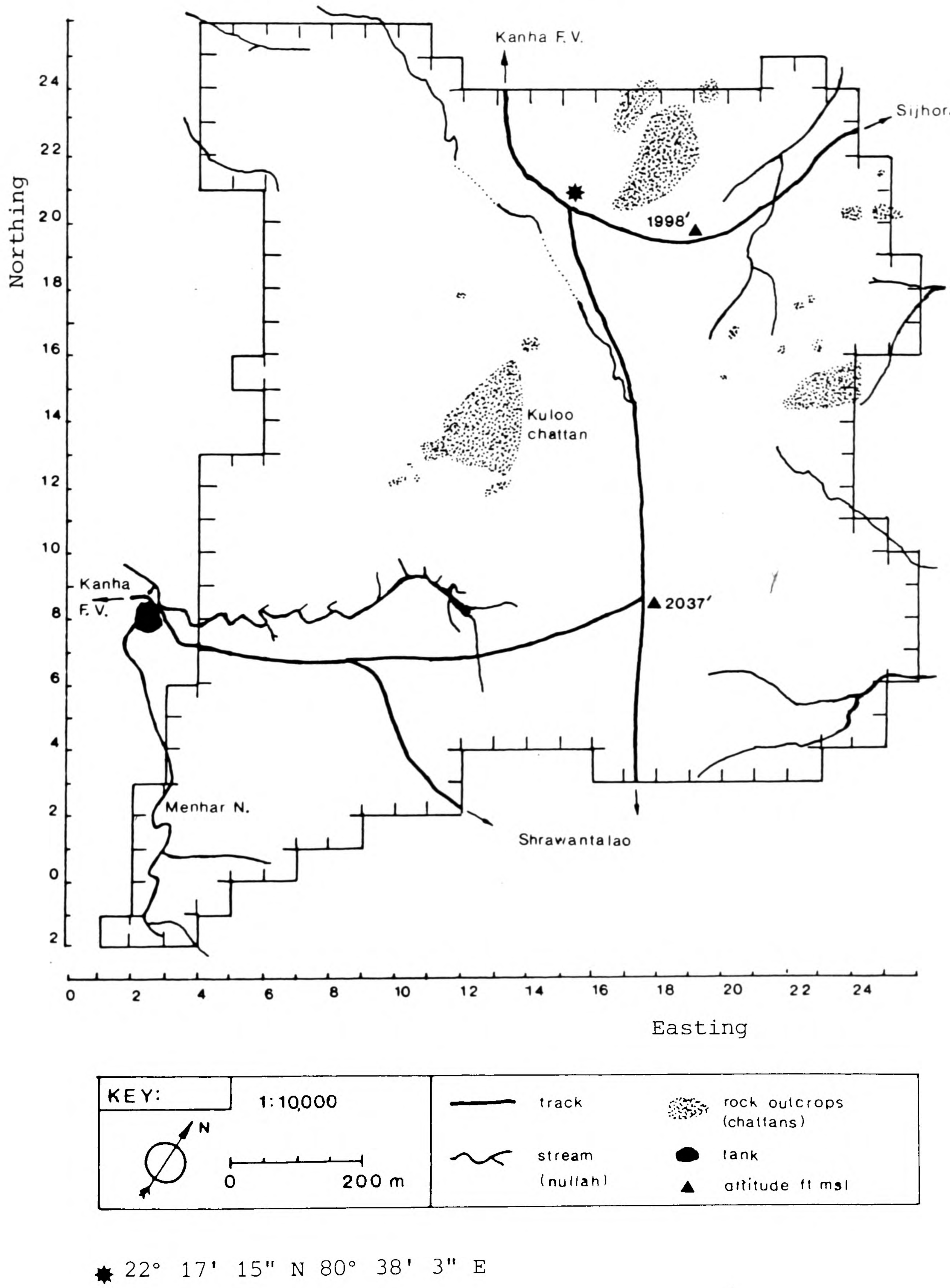


FIG 3.2 SEASONAL VARIATION IN DAYLENGTH AND DURATION OF FIELDWORK DAY.
Daylength data from Astronomical Ephemeris (1981,1982) H.M.S.O.



MAP 6 KULOO CHATTAN STUDY SITE: KANHA MEADOWS.
GRID SYSTEM AND PHYSICAL FEATURES.



✸ 22° 17' 15" N 80° 38' 3" E

MAP 7 KULOO CHATTAN STUDY SITE: KANHA MEADOWS.
HABITAT DISTRIBUTION.

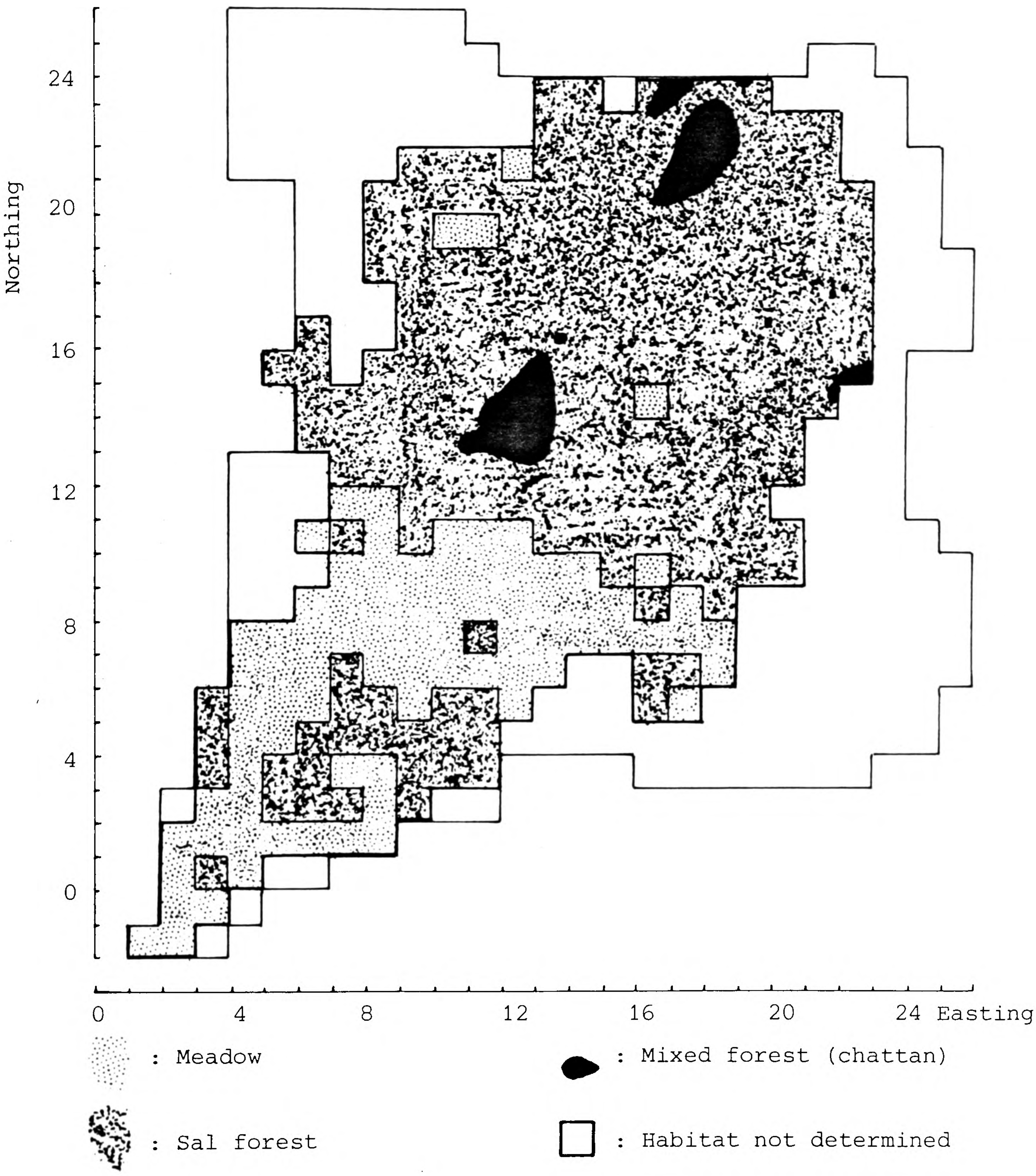


TABLE 3.A SUMMARY OF METHODS

- **FIELDWORK KANHA MEADOWS**
  - VEGETATION
    - Tree phenology
    - Gum phenology
    - Tree enumeration
  - LANGUR
    - Opportunistic monitoring of "C"
    - Population survey Kanha meadows
    - SCAN follows
  - LANGUR + CHITAL
    - DROP follows
    - ASSOC follows

CHAPTER 4

INTRODUCTION TO LANGUR BIOLOGY

CHAPTER 4 LANGUR BIOLOGY.

In this chapter pertinent aspects of langur biology are briefly reviewed. Further details of social organisation are given in Chapter 6 and of ecology in Chapters 7 to 10. More detailed accounts of langur biology will be found in Roonwal & Mohnot (1977), Hrdy (1977b), Struhsaker (1975) and Napier & Napier (1967).

4.1 DESCRIPTION.

The Hanuman langur (Presbytis entellus Dufresne 1797) is one of five species of leaf monkey, belonging to the sub-family Colobinae, found in the forests of south Asia. The Colobinae consist of six extant genera, Colobus in Africa and the langurs, Presbytis, and odd-nosed monkeys, Nasalis, Simias, Pygathrix and Rhinopithecus of south and south east Asia. These, with the baboons, macaques and gueunons of the Cercopithecinae constitute the Cercopithecidae, a major Old World primate family.

The genus Presbytis (Eschscholtz 1821), meaning old woman, contains fourteen species of langur or leaf monkey distributed from Kashmir to Sri Lanka, southern China to Borneo (Napier & Napier 1967). The species studied, Presbytis entellus, the Hanuman, grey or common langur (langur being derived from Sanskrit for long tail) has silvery-grey fur with a black short muzzled face and black feet, hands and ears (see Plates 1, 6, 9, 12). The intensity of grey is variable, with older animals tending to be darker. The ventral surface is generally paler than the dorsal surface, a distinction which is more abrupt in mature males than females. Adult females often have a patch of orange or fawn hair between the nipples. The tail is long, thin, short haired and rope like, with a gradual taper terminating in a variable tuft of hair. The trunk and facial ruff hairs tend to be the longest, but general body hair length is short in comparison to some other colobines such as the black and white colobus (C.guereza). The Singalese P.e.thersites sports long crown hairs gathered into a cone, whilst Indian langurs generally have the crown hair projecting forwards to form a crest above the eyes. Limbs are long and slender which with a deep chest and narrow waist suggest a greyhound form. The buttocks, as in other catarrhines, are capped with horny ischial callosites which in females are separated by a cleft containing the external genitalia. In females the region ventral to the callosites, between the thighs, is black and relatively hairless; it is sometimes dotted with depigmented blotches. Adult males are distinquished by the pink, pad like, perineum sexual skin which, as it does not exhibit cyclic changes, is not comparable to the sexual skin of the cercopithecines (Roonwal & Mohnot 1977). In common with other colobines (except C.badius, C.verus) females lack sexual swellings or any other external morphological manifestation of reproductive state. A mature Hanuman has a head and body length of approximately 0.5 to 1m and a tail length of 0.75 to 1m. Body weights of adults range from 9.0 to 20.9kg in males and 7.5 to 18.0kg in females, with the largest animals occurring in the Himalayas (Roonwal & Mohnot 1977).

Langurs, though essentially arboreal, are the most terrestial members of the genus, spending 20-80% of the daylight hours on the ground (Roonwal & Mohnot 1977). They are capable of prodigious arboreal jumps with recorded leaps of 10-12m obliquely and 4m horizontally (Napier & Napier 1967).

4.2 DISTRIBUTION OF Presbytis SPECIES.

P.entellus has a remarkably widespread distribution, being found from 3660m in the Himalaya, throughout the peninsula to Sri Lanka. In the west it reaches as far as Rajasthan and Gujerat and in the north-east through Nepal and Bengal into mid-Assam (Roonwal & Mohnot 1977). It has recently been reported from Bangladesh (Husain 1974). Roberts (1977) estimates the population in N. E. Pakistan, at the extreme limit of their range, to be less than 200. There are unconfirmed reports of langurs in Afganistan (Oppenheimer 1977). Within this vast range four congeners occur:

a/the Nilgiri langur (P.johnii) in the Western Ghats of south India.

b/the purple-faced langur or wanderoo (P.senex) in Sri Lanka.

c/the capped langur (P.pileatus) in the hills bordering the Bhramaputra River of N.E. India and Bangladesh.

d/the golden langur (P.geei) in the Manas Tiger Reserve of Assam and Bhutan.

These species, especially P.geei, have a much more restricted distribution than P.entellus, are more arboreal, and appear to be markedly more habitat specific, being largely confined to evergreen or moist deciduous forest (Roonwal & Mohnot 1977). In contrast, the Hanuman langur with its pan-Indian distribution, ranges from alpine forests and meadows above the snowline to scrub, dry and moist deciduous forests and rocky xerophytic areas, in addition to agricultural land, villages and temple sites. Unlike its congeners it does not usually inhabit evergreen forests. In addition ten species are known from S.E. Asia: P.obscurus, P.cristata, P.melalophus, P.aygula, P.frontatus, P.rubicundus from Malaysia and Indonesia; P.potenziani from the Mentawi Islands and P.phayrei, P.francoisi from Indo-China (Hrdy 1977b). All appear to be forest dwellers, mostly in evergreen rainforest.

4.3 PALAEONTOLOGY.

The colobines, unlike the cercopithecines, characteristically have a distinctive natal coat, ruminant-like stomach structure and physiology and early postnatal infant transfer, but lack cheek pouches and sexual swellings. The taxon probably arose in Africa some twelve million years ago and the earliest colobine-like fossil is Victoriapithecus macinnesi of the middle Miocene (Szalay & Delson 1979). The first fully colobine fossils are of the genus Mesopithecus which by the early Pliocene, was spread through southern and central Europe, Iran and Afganistan but not apparently as far as the Pakistan Siwaliks (Heintz et al 1981). Anatomical evidence from Greek specimens suggested that it was more terrestial in habit than extant African species. According to Szalay & Delson (1979) this interpretation agrees with the associated palaeoenvironmental evidence which indicates that they were living in steppe/savannah and evergreen forest. Mesopithecus is regarded as near the basal ancestory of Asiatic colobines (Simons 1972). Fossils show high sexual dimorphism (10% in linear dimensions), similar to extant Asian relatives but higher than the more monomorphic African colobines (Szalay & Delson 1979, Hrdy 1977b). Another extinct colobine, Dolichopithecus, perhaps living in the same Pliocene community as Mesopithecus, showed anatomically extreme adaptations for terrestial life and was perhaps a forest floor forager (Szalay & Delson 1979).

By the late Pliocene (4 million years ago) the fossil evidence suggests that colobines had reached south Asia and had diverged from their African ancestors. In East Africa Paracolobus remains are anatomically similar to the contemporary Colobus leaf monkeys. In Asia, Pliocene Presbytis fossils, from the Indian Siwaliks, closely resemble the langurs of today (Hrdy 1977b).

4.4 SUB-SPECIES.

Presbytis entellus has been easy prey for 'splitting' taxonomists with fifteen sub-species differentiated on the basis of coat colour and pattern, hair length, body size and skull measurements (Pocock 1928, Oppenheimer 1977) [The sixteenth subspecies listed by Roonwal & Mohnot (1977), P.e.shanicus, should be regarded as P.phayrei (Roonwal

1979)]. Oppenheimer (1977) suggests that each subspecies may be associated with a cluster of forest types. However, the large number of sub-species seems unwarranted as many of the differentiating characters appear to vary continuously. Vogel (1977) reviewed the subspecific taxonomy and, more realistically, recognised four taxa:P.e.thersites in Ceylon, P.e.schistaceus in the Himalaya, P.e.achates in south India and P.e.entellus in north and central India. By location, Presbytis entellus entellus is found in Kanha.

There are also gross geographical variations in behaviour, the relationship of which to taxonomy is unclear. Roonwal (1979) has investigated the north-south India cline in langur tail carriage. In north India the tail is generally looped forward and in south India and Ceylon looped backwards. In Kanha, the tail is normally carried looped forward, with the tail tip often touching the back (Type 1A, Roonwal 1979), although especially in adult females the tail tip may remain horizontal, well above the back (Type 1B). There are also marked differences in vocal and behavioural repertoires between Himalayan and Rajasthani langurs (Vogel 1971,1973), the genetic and behavioural significance of which is not understood.

4.5 SOCIAL ORGANISATION.

Langurs tend to aggregate into two types of groups: bisexual troops and smaller all-male bands (see Chapter 6). Solitary adult males are rarely encountered in peninsular India. Bands consistently have large ranges that encompass a number of smaller troop ranges. Males' group membership tends to be fluid, whilst the long term social unit consists of overlapping generations of matrilineal relatives (Hrdy 1977b). Females usually remain in the natal troop for life and are probably highly related to other troop females and their offspring. A further distinction, between unimale and multimale troops, is important in terms of male reproductive success and inter-male and inter-group relationships. The terms used in this study to describe langur social grouping are summarized below:

'group' :an aggregate of langurs conforming to Struhsaker's (1969) definition.

'troop' :a number of adult females with one or more adult males and usually with immatures.

'band' :a number of adult and sub-adult males, without females.

'extra-troop' : any male not resident in a troop.

'unimale':a troop containing only one adult male.

'multimale':a troop containing more than one adult male.

4.6 DIET AND DIGESTION.

As suggested by such a wide distribution, Hanuman langurs have a catholic diet, consisting mainly of leaves and fruits but including other phytophases and grass, herbs, gum, insects and earth (see Chapter 9). Unlike the cercopithecines, langurs do not possess cheek pouches but have a complicated sacculated tripartite stomach with an oesophageal groove; anatomy more reminiscent of a ruminant than a primate (Bauchop & Martucci 1968, Bauchop 1978). This structure is also associated with a ruminant-like digestive physiology involving fermentation by anaerobic bacteria (including cellulose digesters). This produces volatile short chain fatty acids and gases such as carbon dioxide and methane (hence a high frequency of belching in langurs). Investigations of the gastric environment of P.cristata by Bauchop & Martucci (op.cit) suggests that such fermentation plays a major role in metabolism and that structural carbohydrates may serve as an important energy source. That the colobine digestive system is unusual is emphasised by the revelation that doses of strychnine, lethal to rhesus macaques, had no effect on Hanuman langurs (Finn 1929).

4.7 REPRODUCTION.

Males probably do not reach sexual and physical maturity in the wild until 5-7 years old, although in captivity it can be 4.5 years (Ronnwal & Mohnot 1977,see Chapter 6). Menarche in females occurs at about 3.5 years and they subsequently cycle at about 30 day intervals (mean 26.8±1 days; Hrdy 1977b). Estrus, which lasts 5-7 days, occurs midway between menstrual periods at about the time of ovulation. Copulations are usually solicited by females 'presenting': drooping the tail, shaking the head rapidly and presenting genitals towards the male (see Hrdy 1977b). The gestation period, as calculated from captive langurs, is about 200±10 days (Hrdy 1977b). Single births are normal although occasionally twins are born (Roonwal & Mohnot 1977). Neonates have pink, unpigmented skin with diffuse dark brown pelage. They are freely given up by the mother to conspecific female caretakers, sometimes within hours of birth. The flamboyant natal colouration gradually changes, with pigmentation of the skin to black and hair to creamy white, producing the adult pattern in 5-6 months. In captivity the longevity record is 22 years (Roberts 1977) although the colobine record is 30 years (Hill 1975). The maturation sequence and definition of age/sex classes used in subsequent chapters is given in Table 4.A.

4.8 CONSERVATION.

The epithet Hanuman refers to the Hindu monkey god Hanuman which in the Ramayana epic, written about 1000 B.C. assists in the recovery of the god Ramas' kidnapped wife Sita from the Ravana of Lanka. Because of the heroic exploits of its legendary forebears langurs are held sacred, their indiscretions tolerated and they are fed, particularly on Tuesdays, by Hindus. The Buddhist and Jain faiths, with their vegetarian principles, also afford langurs protection. As a consequence of these ancient human attitudes, langurs have lived in association with man, in towns and around temples for thousands of years. The importance of the religon of the human population for the fauna is illustrated by the absence of village dwelling langurs in the Moslem areas of Bangladesh (Oppenheimer 1977). In the remoter forest tracts the non-Hindu or partially Hindu tribals hunt langurs for the pot with bows and arrows and dogs (Oppenheimer 1977). Although langurs are tolerated over most of India they frequently do considerable damage to crops and gardens, inviting harassment. This seldom results in injury or death to the monkeys (Mohnot 1971b,Oppenheimer 1977).

With less than 17% of India now forested (Sagreyia 1967) the habitats available to langurs have changed dramatically. However, human tolerance and the langurs' ability to live in association with man has meant that deforestation, apart from desertification, has little affected the overall distribution of the species. Similar changes in the habitats of the more specialist congeners would be expected to affect the populations far more drastically.

As a consequence of deforestation langurs are brought into closer contact with man, perhaps resulting in increased transmission of zoonoses between the two primate species, to the probable detriment of both. Indeed, Presbytis entellus has been implicated as a resevoir of the Kyasanur Forest Disease. In south India this tick-borne arbovirus, which appears to be transmitted between langurs and man, results in mortality to both species (Woodruff & Bell 1978, Rajogopalam & Anderson 1971). Unless such arboviruses become epidemic, oriental relig ons' respect for the Hanuman declines, or deforestation is drastically accelerated, the prospects for the langur seem secure for the near future.

4.9 FIELD RESEARCH HISTORY.

Presbytis entellus is the most studied member of its genus, with nine long term studies and in excess of 70 published papers on wild langurs. With the exception of McCann (1933) most of the pre-1950's langur literature was concerned with taxonomy (Pocock 1928), anatomy (Ayer 1948) and isolated natural history observations (Champion 1927). McCann (1933) identified allomothering, post-conception estrus, breeding seasonality and proposed a scheme whereby multimale troops became unimale in the breeding season.

Long term studies of langurs began with Jay's (1965) research in northern and central India. The location of 17 field studies are shown in Map 8 with the main investigators identified. In the twenty years of field research many thousands of hours have been spent watching langurs, demonstrating considerable variety in many aspects of langur biology. Bibliographies of langur research are contained in Baldwin et al (1975) and Roonwal & Mohnot (1977).

4.10 INTRODUCTION TO LANGUR BIOLOGY : SUMMARY.

1/ Presbytis entellus is a medium sized, arboreal, grey-furred, black-faced colobine found throughout south Asia from the Himalayas to Ceylon, occupying a great variety of habitats.

2/ Two types of grouping occur, all-male bands and bisexual troops, which may be unimale or multimale. Troops are matrilineal and male troop membership is fluid. Band ranges are large, traversing a number of troops.

3/ Diet is diverse and predominantly vegetarian. The stomach is sacculated and, analogous to ruminants, capable of cellulose digestion.

4/ Females mature at half the age of males and cycle monthly. Females solicit copulations and after a 200 day gestation, produce a single pink-skinned, brown-faced infant which is allomothered by female caretakers.

5/ The Colobinae arose in Africa and reached India in the late Pliocene. Of the four extant subspecies the Kanha population belongs, by location, to Presbytis entellus entellus.

6/ The Hanuman langur enjoys Hindu religious tolerance and has, through its adaptability, maintained its distribution despite drastic deforestation.

7/ Presbytis entellus is the most studied member of its genus since intensive field research began in the 1950's. It has been investigated at seventeen sites, of which nine have been long term studies.

TABLE 4.A.DESCRIPTION OF LANGUR AGE/SEX CLASSES.
(Adapted from Dolhinow 1972,Hrdy 1977b,Sugiyama 1965a and Roonwal & Mohnot 1977).

Sex/Age Class	Abbrev-iation.	Age/ yrs.	Weight/ kg.	Description
INFANT-ONE	IN1	0-0.5	1.5	Brown coat colour,skin pink.Altricial,clinging to mother and allomother Skin pigment deposition begins in first week,turning ashen-grey then black within three months.During third and fourth months coat changes to creamy-white,Transformation complete in 5-6 months.
INFANT-TWO	IN2	0.5-1.3	2.5	Creamy-white coat,without grey patches.Frequently suckling,though not allomothered.Progressively more independent,taking solid food.Clinging less frequent.
JUVENILE MALE	JM	1.3-4	5.0	Weaning (complete within 13-20 months).Testicles scrotal.Independent from from mother.Extensive play and interactions with AM.
JUVENILE FEMALE	JF	1.3-3	5.0	Weaning (complete within 13-20 months).Independent from mother.Extensive play and begins to allomother infants.
SUBADULT MALE	SM	4-6/7	9.0	Not sharply demarcated from JM or AM,transitional to maturity.Testes enlarging,bulging snout visible.Little sexual activity, though capable of copulation.Pink perineum a thin strip or not visible.Coat greying.
SUBADULT FEMALE	SF	3-3.5/4	8.0	Not sharply demarcated from JF. Intense interest in infants.Nipples dots.
ADULT MALE	AM	6/7-	16.0	Full adult size,physical and sexual maturity.Canines fully developed Large pink perineum pad.
ADULT FEMALE	AF	3.5/4-	10.0	Reclassified at first birth.Coat greying.Nipples pendulous.Multipars tend to have wide back,sunken eyes and nipples tend to 'go back'.

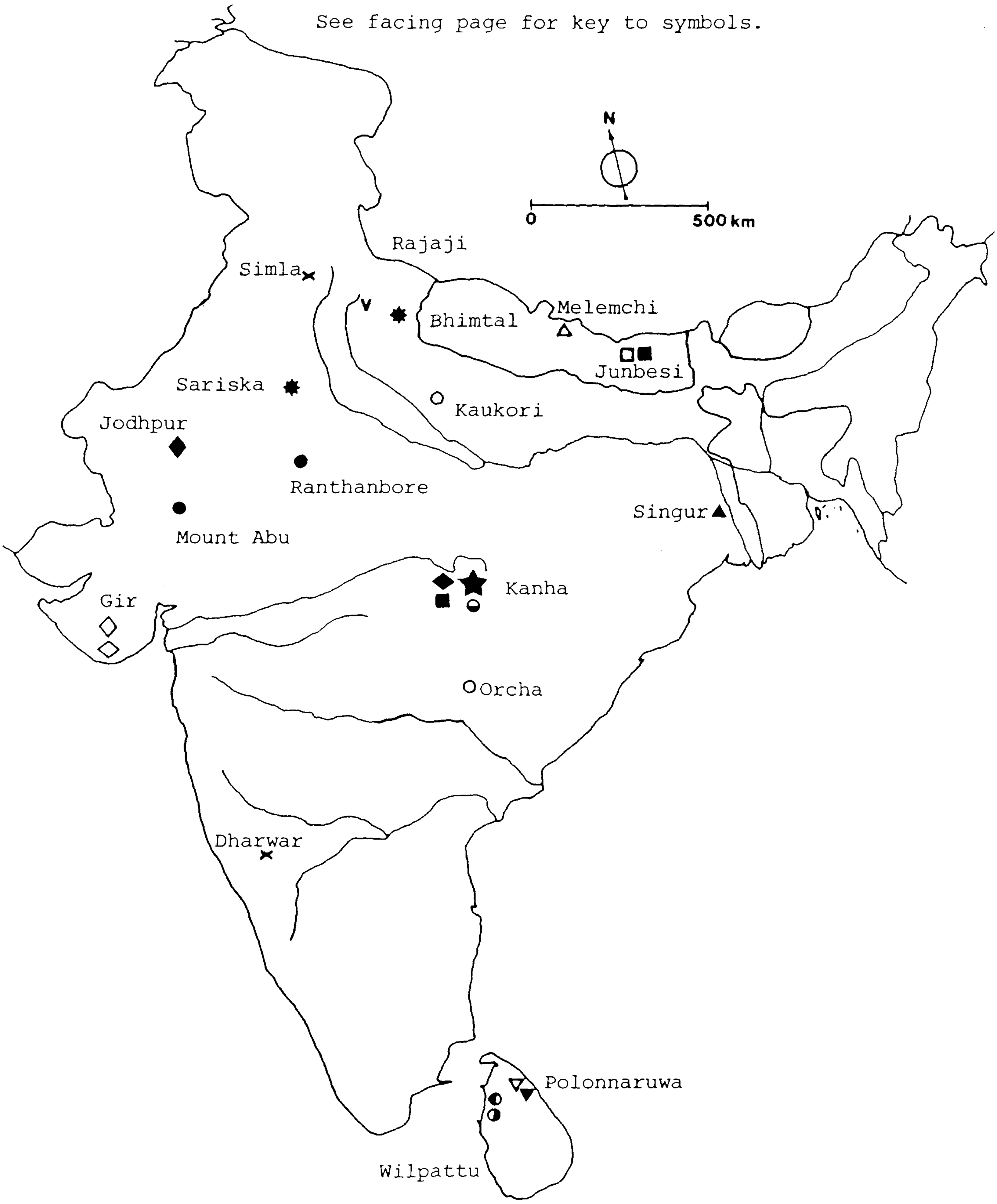
KEY TO MAP 8 (facing page).

SYMBOL	MAIN INVESTIGATORS.
◐	Beck & Tuttle
△	Bishop
□	Boggess
■	Curtin
▽	Hladik
●	Hrdy
○	Jay (= Dolhinow)
◆	Kankane
⊖	Lohri & Nagel
♦	Mohnot
◑	Muckenhirn
★	Newton
▲	Oppenheimer
◇	Rahman
▼	Ripley
◇	Starin
×	Sugiyama
✸	Vogel
V	Vonder Haar Laws

MAP 8 : MAJOR Presbytis entellus STUDY SITES 1958-1982.

INDIA,NEPAL AND SRI LANKA.(see MAP 1 for details)

See facing page for key to symbols.



CHAPTER 5

VEGETATION ECOLOGY

CHAPTER 5 VEGETATION ECOLOGY.

5.1 INTRODUCTION.

Langurs spend the majority of their feeding time consuming vegetable matter derived from trees whether it be leaves, fruit, gum or invertebrates. Therefore, the species of tree present, their abundance, spatial pattern and phenology are likely to affect langur feeding ecology, ranging and social organisation. Indeed, other investigations of colobines suggest that such relationships are important (Clutton-Brock 1977a, Oates 1977a, Struhsaker 1975, Marsh 1981b). In this chapter the ecology of the vegetation inhabited by the study troop is described as a framework within which langur feeding, ranging and activity will be considered in subsequent chapters. The natural history of the vegetation is also considered in Chapters 2 and 3.

Previous work on the flora of Kanha has concentrated on reserve-wide surveys and not on the investigation of small patches of forest. Brander (1906) described the forests, logging operations and the successional processes involved in the recolonization of the anthropogenic meadows. Puri (1960) examined the floristic composition and soils of Madhya Pradesh sal forests including sites within Kanha. Maheswari (1963) and Schaller (1967) surveyed the flora of Kisli and Kanha Ranges and produced incomplete inventories of species present. Panwar (n.d.) classified the vegetation according to the forest types of Champion & Seth (1968, see Chapter 2) and describes the distribution of plants across the reserve. Martin (1977) and Martin & Huber (1973), whilst investigating the ecology of the barasingha, examined the grass flora of the meadows of Kanha range. Correlation analysis was used to identify grassland associations and meadow tree density and its relation to succession were discussed. Kotwal (n.d.), acting on the recommendations of Sykes & Horrill

(1977), investigated the community structure of meadow and forest using line transects and hectare plots in a reserve-wide survey. Kotwal & Pandey (1981) estimated meadow grass production and herbivore consumption. Dr. Kotwal has additionally amassed a large herbarium of plant specimens at Kanha village.

5.2 METHODS.

Forest ecology was investigated in relation to "C" troop biology and therefore the area studied was the annual range of "C" (74.5 ha.). The grid system used was identical to that used in recording ranging (see Chapter 3 & 8). Two sets of data were collected, the enumeration of tree composition and monthly monitoring of tree phenology.

5.2.1 ENUMERATION OF TREE COMPOSITION.

All trees, defined as woody plants >2m in height, within the annual range of "C" troop were enumerated. During the cold weather of 1981/82 each quadrat was visited and every tree identified to species and the girth at breast height (1.3 m) measured to the nearest cm. In those species with multiple trunks (e.g. the buttresses of Ficus species) the girth of each trunk was measured separately. To prevent multiple measurements being taken of the same tree in densely forested quadrats, a chalk mark was made on the south side of the tree bole once tallied. If a tree could not be identified, due to the absence of a relevant plant part, a note was made of its location and it was (with two exceptions) identified during a subsequent phenological stage. Tree identity was determined with the help of Mungal and Mohan Baiga using vernacular names and the floras and lists of Brandis (1874), Witt (1916), Kotwal (n.d.) and Maheswari (1963). Dr P.C.Kotwal of the Madhya Pradesh Forest Department and Mr Radcliffe-Smith of Kew Botanic Gardens kindly checked identities and determined problematic specimens. I constructed a herbarium of specimens from the study area which will, at some future date, be deposited at Kew.

5.2.2. TREE PHENOLOGY.

For the recording of tree phenology a measure was required which, although simple to use, would indicate the quantity of each phytophase available on each species in each month. Direct counts of items would not have been possible and so the crown density method devised by Koelmeyer (1959) and developed by Struhsaker (1975) and Marsh (1981c) was used. At the start of phenology recording it was not known which species were important in langur feeding and therefore all species occurring within the known "B" and "C" ranges and a 200m surround were sampled. Where possible four individuals of each species were monitored. These trees were selected using a stratified random sample. The range was divided into four quarters and at a location within each quarter, determined from random number tables, a bamboo stake erected. With each stake as the origin, I walked a close spiral and the first living specimen of each species encountered was recorded and tagged with a numbered aluminium label. A total of 61 species of tree and woody climber consisting of 215 individuals was sampled. Some species were represented by less than four individuals in the study area and as a few species were discovered in the area during the monitoring a mean of 55 species were recorded per month. The phenology sample is detailed in Appendix II.

Each month, between the DROP and SCAN 'follows' (see Chapter 3.2) two days were spent visiting each tree of the phenology sample. Each plant was examined both from a distance with binoculars to see to the canopy top and closely to examinine the individual items' density, size, colour and texture. The ground below the canopy was checked for items, fallen from the tree, which may have been missed in the canopy. I visually estimated the abundance of each phytophase present relative to the maximum abundance expected for that species, the crown density of Koelmeyer (1959). This assessment was based on the experience gained during the 1980 field season and expressed on a linear 0-4 scale. A score of 4 referred to the maximum observed density of a particular phytophase for a given species. Values of 3 (some), 2 (few), 1 (very few) indicated densities 75%, 50% and 25% of the maximum respectively.

Though subjective this method was quick and simple to record; any more objective method would have required considerably more time than was available.

The phytophase categories recognised (after Struhsaker 1975, Marsh 1981c) were:

Mature leaves -full size with mature texture and colour. (often leathery and dark green)

Young leaves -full size with immature texture and colour (often soft and light green).

Open leaf buds-lamina uncurled from bud but less than full size, with immature texture and colour (often soapy and pink or very light green).

Leaf buds -lamina curled within closed bud.

Flower bud -flower curled within closed bud.

Flower -flower parts uncurled from bud.

Fruit -all types of fruit, unripe and ripe.

5.3 FOREST STRUCTURE.

5.3.1. FOREST STRUCURE : RESULTS.

Within the 74.5 ha study site 9935 trees were enumerated, consisting of 62 species of tree (including two unidentified specimens) and 6 species of climber. All species were indigenous apart from teak *Tectona grandis* which was planted in the NW part of the study area (see

3.1). As described in Chapter 3, three vegetation types were identified. The distribution of meadow (27.5% of study area), dry deciduous forest (3.3%) and sal forest (69.2%) is shown in Fig. 5.4. A sal forest profile from the study area is depicted in Fig. 2.3. The canopy occurred between 15 m and 30 m and consisted largely of sal with common associates being Pterocarpus, Terminalia, Adina, Mitragyna and Anogeissus. A sub-canopy could be distinquished of shorter trees such as Stereospermum, Syzygium, Ficus, Lannea, Buchanania and Bauhinia retusa. Below these there was a bush stratum containing species such as Cassia, Diospyros, Cordia, Mallotus, Ehretia and Saccopetalum. The results obtained using different measures of tree abundance and dispersion are considered below; the data are summarised in Table 5.A, 5.B.

A/ Density.

The density of trees over the entire tract was 33.34 individuals per 0.25 ha quadrat (range 0-109) or 133 /ha (0-436 /ha.) The predominant species was Shorea with 3878 trees or a mean of 13 per quadrat (range 0-100). The frequency distribution of abundances shows a marked decline with descending rank (Fig 5.1) such that by rank 20 only 200 trees were tallied per species. Half the species were represented by less than 20 trees. Owing to the preponderance of sal the family with the highest density was the Dipterocarpaceae (Table 5 B). Relative density is defined as :

$$\text{Relative density species } i = \frac{\text{Number of individuals species } i}{\text{Total number of individuals of all species}} \times 100$$

Shorea constituted 39% of relative density whilst the next rank, Lagerstroemia, contributed only 13% (Table 5.A). Only 12 species had a relative density of greater than 1 %. A species:area curve is plotted in Fig 5.2, calculated by recording the cumulative sum of species recorded from the area as quadrats are successively added in random order. The curve approaches an asymptote at about 25 ha suggesting that the area sampled was sufficiently large to be representative of the forest composition of the area.

The number of indivduals of the six species of woody climber recorded in the 74.5 ha area were:

Zizyphus rugosa	20	Ficus parasitica	3
Bauhinia vahlii	14	Butea superba	1
Ventilago calyculata	5	Ichnocarpus frutescens	1

B/ Dominance.

Dominance or basal area (Grieg-Smith 1983) includes more information than density by taking into account tree size. From the measurements of tree girth at breast height the cross-sectional area at breast height (ABH) was calculated for each tree and summed for each species over the entire area. Dominance, expressed as ABH in m^2, can be visualized as the area of the stump tops remaining if the forest were clear-felled at breast height. Relative dominance is defined as:

$$\text{Relative Dominance species}^{\,i} = \frac{\text{Dominance of species}^{\,i}}{\text{Sum of dominance values of all species}} \times 100$$

The total area at breast height for the entire forest was 1038 m^2 and therefore a mean of 3.48 m^2 per quadrat. As well as being abundant, sal is one of the largest trees present (up to 32m in height) and hence is the leading dominance rank with an ABH of 627m^2 and a relative dominance of 60% (Table 5.A). The second rank, Lagerstroemia, has a relative dominance of only 8% and only the top 12 ranks exceeded 1%. The frequency distribution of dominance is therefore similar to that for density plotted in Fig 5.1. Owing to the abundance and size of sal the Dipterocarpaceae, though represented by only one species, leads in family dominance (Table 5.B).

The relationship between relative dominance and relative density, for the top 20 ranks of the former, is shown in Fig 5.3. This illustrates how some species, such as Cassia fistula, although very abundant, contribute very little to dominance due to their small size. In contrast a very few species, notably Ficus tomentosa, although of very low density, have a high relative dominance, on account of their vast girth.

The distribution of dominance per quadrat for all trees is shown in Fig 5.5 and for selected species in Figs 5.6-5.15. These three-dimensional (3-D) plots, produced by GINOSURF (CADcentre 1983) on the OUCS VAX computer, omit the 7 negatively numbered quadrats in the south-west corner of the study area. For comparison with the 3-D plots, Fig 5.4 gives the absolute x and y coordinates, the grid-cells sampled and the distribution of habitats. Boundaries and habitat information cannot be easily superimposed onto the 3-D plots because the z-values are drawn from the grid line intersections, and not from the centre of quadrats.

The plot of dominance for all trees (Fig 5.5) shows the meadows and the paucity of trees, particulary sal, on Kuloo chattan. Shorea (Fig 5.6) is confined to the main block of forest and only occurs on the meadows as small copses of 'poles' or solitary 'nurse' trees (Chapter 2,Brander 1906). The distribution of sal mean ABH per grid cell (Fig 5.7) suggests that consistently thinner trees occur in the east and thicker, but more variable sized, trees in the west. Saccopetalum (Fig 5.8) is found throughout forest and meadow but with especially high dominance in a small patch in the west. Syzygium (Fig.5.9) is also spread over the entire range but with particularily high dominance in the north-east. In contrast Lannea, Schleichera, Ficus tomentosa and Sterculia (Fig 5.10-13) all have distributions resticted to the chattans; Lannea also spreads among the isolated boulders peripheral to the rock outcrops. In contrast, Butea and Bombax (Fig 5.14,15) tend to be confined to the meadow areas. These distributions support the division of the study area into meadow, sal (with associates) and chattan mixed forest as natural groupings of tree species.

C/ Frequency.

Frequency (Grieg-Smith 1983) is a description of the uniformity with which tree species are distributed across the tract and is expressed as the number of quadrats containing a given species ('rooted frequency' of Kershaw 1973). Alhough a useful measure, the value obtained is dependent on quadrat size, plant size and the spatial distribution of trees (Kershaw 1973). The frequency and relative frequency, using a 0.25 ha grid cell size, of each species is shown in Table 5.A. Relative frequency is defined as:

$$\text{Relative frequency of species}^{i} = \frac{\text{Frequency of species}^{i}}{\text{Sum of frequency values for all species}} \times 100$$

The most ubiquitous tree was Lagerstroemia, occupying 219 quadrats with a relative frequency of 9.55%. Cassia and Shorea rank second and third respectively. Only eight species occupy more than 25% of the quadrats and twenty one species occurred in less than 10 grid cells. The frequency distribution of relative frequency is similar to that for density and dominance.

D/ Importance Value Index.

The Importance Value Index (IVI) incorporates relative density, dominance and frequency in a single index, giving an indication of the importance of each species in the stand (Grieg-Smith 1983). IVI was calculated by summing the three relative percentage measures, giving a maximum possible value of 300 (Kershaw 1973). The higher the density, the larger the tree and the more ubiquitous a species the higher the IVI. The IVI's for the study area are shown in Table 5.A. with Shorea the leading dominant at 107. The succeeding ranks are Lagerstroemia with 31 and Cassia with 16. Twenty three species had IVI's less than 1. As with the previous measures, ranking of IVI indicates a forest in which a few species are very important and most species contribute little to overall forest structure and biomass.

E/ Dispersion.

The degree of spatial clumping, or dispersion, of tree species can be summarized by classifying the pattern of individuals as regular, random or clumped (Grieg-Smith 1983). Of the numerous tests available for detecting departures from randomness the variance:mean ratio (V/M) has been used here as recommended by Greig-Smith (1983). The V/M ratio, or coefficient of dispersion, utilizes the equality of the mean and variance for items randomly dispersed according to the Poisson distribution. A ratio of less than 1 suggests a regular dispersion but if greater than 1, a contagious or clumped pattern. This measure is applicable for species which are neither very rare or very common (Grieg-Smith 1983). The latter condition arises because for the Poisson distribution to be applicable, the tree density should be small relative to the maximum possible. In species such as Shorea this condition would be violated and the item distribution would approximate to a binomial and not a Poisson (Grieg-Smith 1983). The V/M ratio for species with greater than 20 trees in the stand are given in Table 5.A. The significance of departures of the ratio from 1 can be tested by comparing the departure with its standard error, by means of a t-test (Grieg-Smith 1983). Significant departures from unity are indicated if the ratio differs by greater than 0.256 from 1 (N=298, s.e.= 0.082, for $p<0.001$, t=3.1176). Therefore a V/M > 1.256 indicates a clumped distribution and a V/M < 0.744 a regular pattern.

Of the 41 species for which V/M was calculated 36 were significantly clumped and the distribution of 5 could not be distinguished from random. The most highly clumped species were Lagerstroemia and Tectona. By inspection, species such as Sterculia, Ficus tomentosa and Lannea were also clumped (see Fig 5.10,12,13) but were too rare to calculate a meaningful statistic. The five species which were demonstrated to have a random-like distribution were Ficus infectoria, Pterocarpus, Terminalia balerica, Albizzia and Stereospermum xylocarpum, which are all large canopy trees noted in the field as having scattered distributions. No species showed a distribution that departed significantly from random towards a regular dispersion, although the test is less sensitive to some such patterns. The ratio is also only applicable to the 0.25 ha grid size as, like all such statistics, it is sensitive to quadrat size (Grieg-Smith 1983).

5.3.2 FOREST STRUCTURE: DISCUSSION.

The detailed enumeration of forest structure supports the division of the study area into three habitat types: sal forest, mixed forest and meadow. The meadow could also, by analogy with Dinerstein (1979), be regarded as 'Bombax savannah' with Butea and Lagerstroemia as common associates. Within the forest most species showed clumped dispersions, with a few large species scattered in a random-like distribution. Much of the clumping arose from the specificity of some species to the chattans, forming islands of mixed forest. The pattern, probably caused by differences in superficial geology, illustrates on a small scale the distribution of sal and mixed forest across the entire reserve (see Chapter 2). Around the chattans the forest is dominated by the abundant and large Shorea. This preponderance is characteristic of the species (Puri 1960), which ranges over much of north and central India. Dinerstein (1979) found a relative dominance for Shorea of 60.1% in the Nepalese terai. Champion & Seth (1968) state that sal constitutes 60-90 %

of the canopy trees where it occurs but they consider that its dominance had been intensified by human activities. Although sal is more 'aggressive' than its associates and naturally predominates as the climatic climax, forest management has by selective removal of other species increased its abundance (Champion & Seth 1968). The propensity of sal to form near single species stands is also emphasised by the IVI values: for sal the value was 107, whilst it was only 31 for the second rank, <u>Lagerstroemia</u>.

The dominant family in the study area was the Dipterocarpacae but only by virtue of the abundance of <u>Shorea</u>. Dittus (1977) found a similar pattern in Sri Lankan semi-evergreen forest which was dominated by <u>Drypetes</u> (IVI=55.5) with most of the other 63 species rare. These south Asian maximum IVI's are intermediate between those of rainforest (e.g. 23 in Brazil, 14 in Brunei) and those of temperate woodland (e.g. 228 in Winsconsin, Dittus 1977). The sal forest also contrasts with other Asian Dipterocarp forests, mostly rainforests, which have higher species diversity and lack single dominant species (Richards 1979).

The sal forest differs substantially from the mixed forest of the hills and chattans in which the maximum IVI is considerably lower with no single species predominating. Kotwal (n.d.) compared forest structure between the two habitats by enumerating all trees (plants >30cm girth at breast height) in hectare plots, two in each habitat. The data, reproduced on the following page, demonstrates the higher tree density, lower species richness and single species domination of the sal forest in comparison to the mixed.

	Sal Forest		Mixed Forest	
Plot	1	2	1	2
Tree density/ha	523	482	417	408
No. of species/ha	16	14	28	26
Most abundant species	Shorea robusta		Casearia graveolens	Bauhinia retusa
Relative dominance of dominant/%	87.2	73.2	26.4	15.7

Martin (1977), in surveying sal forest structure adjacent to the meadows, found that Shorea comprised 52-55% of all trees. In this study only 38 % of trees were Shorea, although if meadow and chattan vegetation was excluded and trees were defined as those with a girth in excess of 30cm this species would probably contribute 50-60% of individuals.

As discussed in Chapter 2 the meadow is the result of Baiga bewar cultivation of unknown date, but prior to 1868. The open area is maintained by frost and grazing and until recently by annual fires. The tree composition of the meadows can be divided into two components. The older large, typically forest trees, such as Shorea, Terminalia, Ficus and Madhuca today act as 'nurse' trees (Brander 1906) and appear to be relicts from the original vegetation, spared the axe during bewar. Species such as Butea, Bombax and Zizyphus appear to be less typical of forest and have probably colonized since the abandonment of the meadows. The relict species also contrast with the invaders in being important in the Baiga economy, providing cooking oil, medicine, food and whisky raw material (Mungal pers.comm.). Perhaps the Baiga spared from felling a selection of such desirable trees as a perennial source of commodities and shade. The distinction between meadow relicts and colonizers is also supported by data in Martin (1977) which indicates that the Kanha meadows differ from nearby, more recently abandoned meadows in having larger trees, lower tree density and fewer typically forest trees. There are signs of successional encroachment of the meadows at ecotones and as patches of Butea bushes and Diospyros saplings. With the cessation of deliberate burning in 1972 the proliferation of frost and browse resistant species, previously held back by fire would be expected.

Sal forest is the climatic climax for the low lying land of the region (Champion & Seth 1968) but its structure is likely to have been affected by forestry operations. The study area formed part of Brander's (1906) working plan and selective sal fellings were scheduled for 1912-13 in Compartment 756. In addition, from 1937 to 1958 1024 sal in the compartment were felled in operations to control cerambycid beetles. In 1942, 1944 and 1955 5344 drought affected trees were felled and 1088 cerambycid attacked trees were removed between 1944-50. In 1935 and 1936 an unknown number of sal were felled in improvement fellings and in 1942-44 16 Pterocarpus were logged (Compartment History 1962). As the 281 ha Compartment 756 contains the 74.5 Ha study area, an unknown proportion of these fellings occurred within the forest enumerated in this study. The uniformly thin sal trees in the east and thicker but more variable sized trees in the west suggest the possibility that the eastern part was clear-felled whilst the western section was selectively logged. Forest Department management also involved the cutting of climbers, especially Bauhinia vahlii, from the trees.

During the millenia of undisturbed Baiga culture, the tribals are likely to have altered vegetation structure by forest exploitation, in addition to bewar. In particular tapping of sal for 'rall' resin, debarking of Ougenia for fish poison and Cordia for rope and felling other species for timber and firewood would over such a time period be expected to have altered forest composition. Similarly, the preservation of Madhuca for whisky ('daroo') production and certain trees for religious reasons would seem likely to have increased their representation in the forest.

The sal forest about the Kanha meadows should therefore be regarded as secondary and not primary. It is however representative of the habitat in which langurs have lived for many thousands of years and is in considerably more pristine condition than other forests in the Central Indian Highlands.

5.4 FOREST PHENOLOGY.

5.4.1 FOREST PHENOLOGY : RESULTS.

The monitoring of phenology produced monthly indices of abundance for each phytophase on 215 trees. The mean value of the index for four trees per species for each month and phytophase is plotted for the top eight species in terms of density in Fig 5.16,17. Comparisons should only be made within items as the biomass present for a given score will vary substantially between items. The pattern of leaf and reproductive phenology over the annual cycle is considered below.

A/ Leaf phenology.

All species had one major period of leaf renewal during the year cycle, between February and August. Most species abscissed between February and April, flushing between April and June. There was wide variation in the extent and duration of low leaf density i.e the degree of deciduousness. There is a gradation and not a sharp distinction between evergreen and deciduous phenology. Categories were distinquished, in the manner of Koelmeyer (1959), on the basis of the intensity of leaf depletion:

Deciduous :mean phenological index ('crown index') for leaves (young & mature) falling to 0 or 1 during one or more months.

Semi-evergreen:mean leaf phenological index not falling below 2 in any month.

Evergreen :mean leaf phenological index not falling below 3 in any month

By the above definitions one species, Ficus cunia, showed an evergreen pattern, represented by only one individual, which renewed its leaves in March and April.

Four species of tree (Shorea, Syzygium, Mallotus and Casearia tomentosa) and one climber, Ventilago, showed a semi-evergreen pattern. Shorea (see Fig 5.16) dropped its mature leaves in a relatively brief period in February and March and the canopy flushed concurrently producing a mean score of 4 for young leaves by March. Syzygium and Casearia showed a similar but a more extended leaf renewal. Mallotus showed the least intermonthly variability in phytophase index with all ages of foliage present in each month. Although leaf buds were produced in every month, leaf renewal peaked in May to July. A regular sudden drop in stream water level in March appears to be a consequence of a surge in water demand by sal trees flushing synchronously (H.S. Panwar pers.comm., pers.obs.)

The remaining 55 tree and climber species in the forest were deciduous. A few species such as Bombax, Lannea and Sterculia abscissed in the winter months of November to January, whilst others such as Adina and Gardenia retained mature leaves until the end of the hot weather. However, most species shed their leaves between March and May and came into mature leaf by June to August. Sterculia was particulary unusual in that leaf fall occurred in November and December and with renewal in

July and August, the canopy was without its enormous leaves for most of the year. Whilst showing a deciduous pattern, a few species (Terminalia tomentosa, Anogeissus, Ficus tomentosa, Zizyphus xylopyra and Bauhinia racemosa) also tended to produce leaf buds throughout the year with a peak in production after leaf fall.

Therefore, the predominant phenological pattern was the deciduous renewal of leaves between the winter and hot weather. A few semi-evergreen and a solitary evergreen species renewed foliage during the same season. No species showed prominent leaf fall during the monsoon.

B/ Reproductive phenology.

As with leaves most trees had only one major period of flower production in the annual cycle, for most species this was concentrated within the hot weather months of April, May and June. Notable exceptions were Bombax and Ehretia, which flowered in February and March and a group of eleven species (Litsea spp., Adina, Semecarpus, Bridelia, Bauhinia retusa, Pterocarpus, Mallotus and Tectona, Embelia and Ventilago) which flowered in the monsoon and early winter months between July and November. Therefore 41, of the 52 species which were observed to flower, reproduced whilst the canopy was deciduous.

Most species fruited in the month following the maximum flower score but in Albizzia and Terminalia there was an interval of four months. Gardenia, Adina, Mitragyna and Lagerstroemia tended to retain dehisced post-reproductive fruits on the tree between flowerings.

The majority of species therefore appeared to follow a simple annual cycle, with reproduction occurring during the hot weather deciduous phase. However, the pattern for Ficus species appeared to be more complicated. The evergreen Ficus cunia produced figs continually. Figs were present in most months on F.arnottiana, infectoria and tomentosa. However, the plots indicate two reproductive cycles a year, six months apart, with fruiting peaks in the hot weather and late monsoon for F. arnottiana and mid-monsoon and winter for F. infectoria and tomentosa.

C/ Availability index.

The phenological patterns of each species were aggregated to give an availability index for each phytophase, for each month, for the entire forest. This was computed, using an adaptation of Marsh's (1981c) index, by weighting the mean phenological score per species for each month by the species' relative dominance :

$$AI_n = \Sigma (A_i x RD_i)$$

where

AI_n = availability index for a given phytophase for n species.

A_i = mean phenological score of the phytophase for species ^{i}.

RD_i = relative dominance of species ^{i}.

The monthly fluctuations in the availability index, calculated for the 49 tree species with a complete record, are tabulated in Appendix V.H and shown in Fig 5.18 and for these species but excluding Shorea in Fig 5.19. The plots agree with the above descriptions of individual species phenology. The forest was relatively leafless from March to May as leaf buds burst and flowering occurred. Fruiting peaked in May but had a wider temporal distribution than flowering, which was prevalent only from March to May. If the effect of the leading dominant, Shorea, is removed the availability index shows a longer leafless period and less restricted reproductive activity. With Shorea omitted from the sample, peaks are less pronounced and the variation smoothed, with substantial fruiting evident outside the hot weather. Comparison of these two plots of availability index demonstrates the effect a dominating tree with rapid, brief semi-evergreen phenological changes has on predominantly deciduous community phenology.

5.4.2 PHENOLOGY DISCUSSION.

The results of phenology monitoring suggests a forest in which change is largely confined to the four hot months of March to June. The trees change little in phytophase crown density at other seasons and in the monsoon phenology is relatively invariant. This community synchrony suggests that individual species patterns are being entrained by the pronounced seasonality of the environment. With only a fourteen month run of monitoring, seasonality must be implied with caution but the observations of Brandis (1874,1906) and Witt (1916) with the long term studies (see below) suggest that the rhythmn described here is common in south Asia and is seasonal. Therefore, the 1981/2 monitoring is likely to be representative of many past years in Kanha. More than one annual cycle is necessary to investigate the nature of the environmental factors influencing phenology. However, the lengthy studies of Krishnaswamy & Mathauda (1954) and Koelmeyer (1959) in south Asia suggest that climatic variables such as temperature, humidity and rainfall are important determinants of the timing of phenology patterns.

Dinerstein (1979) investigated tree phenology in Nepalese terai sal and riverine forest and found that most species were deciduous, with 86 % of the 43 species renewing leaves during the hot and cold weather. Also 50 % of the species flowered during the hot weather, giving a pattern similar to that described for Kanha. There have been two long term phenological studies in south Asia which include species also found in this study. Krishnaswamy & Mathauda (1954) monitored trees at the New Forest, Dehra Dun in the Himalayan foothills for 19 years and Keolmeyer (1959) investigated 2000 trees in Ceylon for 10 years.

The plots of Tropical Dry Mixed Evergreen Forest in Koelmeyer's study shared eight species with Kanha. Although 40 species were deciduous the forest was dominated by Hemicyclia (62 % of trees) which, by analogy with *Shorea*, gave the evergreen character to the forest. The maximum incidence of leaf fall was during the two dry seasons per year and aridity was suggested as the trigger for foliar change. Of the species shared between the two study sites all were similarly classified as deciduous or semi-evergreen apart from *Schleichera*. Unlike its deciduous character in Kanha, Keolmeyer found it to be evergreen with its characteristically dense crown due to extended flush, independent of leaf fall.

Krishnaswamy & Mathauda (1954) recorded the dates of occurrence of phenological events for five individuals each of 17 species, with 8 species common to Kanha. They found that the main period of foliar renewal was from January to May with flowering in late winter and early summer producing fruit in the pre-monsoon or monsoon months. The shared species were similarly classified as deciduous and although Kanha semi-evergreen species were classified as evergreen, the difference is probably only due to terminology. Trees showed the same temporal relationship between foliar and reproductive phenology. The sequence of abscission, flowering, flush and fruiting is the most frequently encountered for deciduous trees (Raemakers *et al* 1980).

In contrast to the synchronous deciduous and semi-evergreen patterns in central Indian Dipterocarp forests, rain forests dominated by the same family tend to have more intermittent, asynchronous phenology with lower rates of change. The problems inherent in lumping tropical forests together under one category of 'forest' are exemplified by comparing the reproductive phenology in Kanha with that of the Kibale forest. In this Ugandan moist evergreen forest most tree species fruited asynchronously, non-seasonally or synchronously but very rarely (Waser 1975); a very complicated and diverse set of patterns quite different to the phenology of sal forest. If phenology patterns exert a strong influence on arboreal primates, as seems likely (Clutton-Brock 1977a), cercopithecids in Kanha and Kibale are likely to have very different inter-relationships with their forest habitat.

This method of evaluating phenology, devised by Keolmeyer (1959) was found effective in efficiently producing quantitative information. It yielded considerably more data than simple presence/absence recording with little extra effort. It enabled objective definitions of deciduousness and the calculation of a summary index of community phytophase availabilty. Any more sophisticated technique, perhaps involving counting items, would have involved a prohibitive time investment. The sample size of 4 trees per species was, with low intraspecific variabilty, probably sufficient.

In conclusion, analysis of a patch of sal forest showed it to be dominated by Shorea but it also contained scattered islands of mixed forest on chattans. The forest is probably largely secondary and has been broken up by previous cultivation. Tree phenology was strongly seasonal and deciduous, with reproduction occurring mostly during the leafless hot weather phase. The information on forest structure and phenology is integrated with data on feeding and ranging in Chapters 8, 9 and 10.

5.5 VEGETATION ECOLOGY : SUMMARY.

1/ All 9935 trees within the 74.5 ha forest and meadow mosaic of the "C" troop annual range were enumerated. Measures of density, dominance, frequency, dispersion and importance value were calculated using a 0.25 ha grid system. The tract was dominated by Shorea robusta (60% relative dominance) with most of the other 60 species rare. Twenty-three species had Importance Value Indices of less than 1.

2/ Five large canopy tree species were scattered through the forest with a random-like dispersion. Most common species showed clumped distributions, especially those species characteristic of mixed forest which were restricted to the chattans.

3/ The meadows contained relict forest trees, possibly spared during clearances, and colonizing species not found within the forest.The evidence of past logging and Baiga exploitation suggests that the forest is largely secondary.

4/ The phenology of 215 individuals, representing all tree and climber species, was monitored monthly, using an index of phytophase abundance.

5/ Leaf renewal was highly synchronous between and within species and occurred predominantly between February and June. Flowering generally occurred whilst leafless and fruiting a month later in the hot weather and early monsoon.

6/ One species was classified as evergreen, five as semi-evergreen and fifty-five as deciduous.

7/ An availability index was calculated for each phytophase as the sum of individual species patterns weighted by species dominance. This demonstrated the influence of the semi-evergreen leading dominant, Shorea, on the otherwise predominantly deciduous phenology.

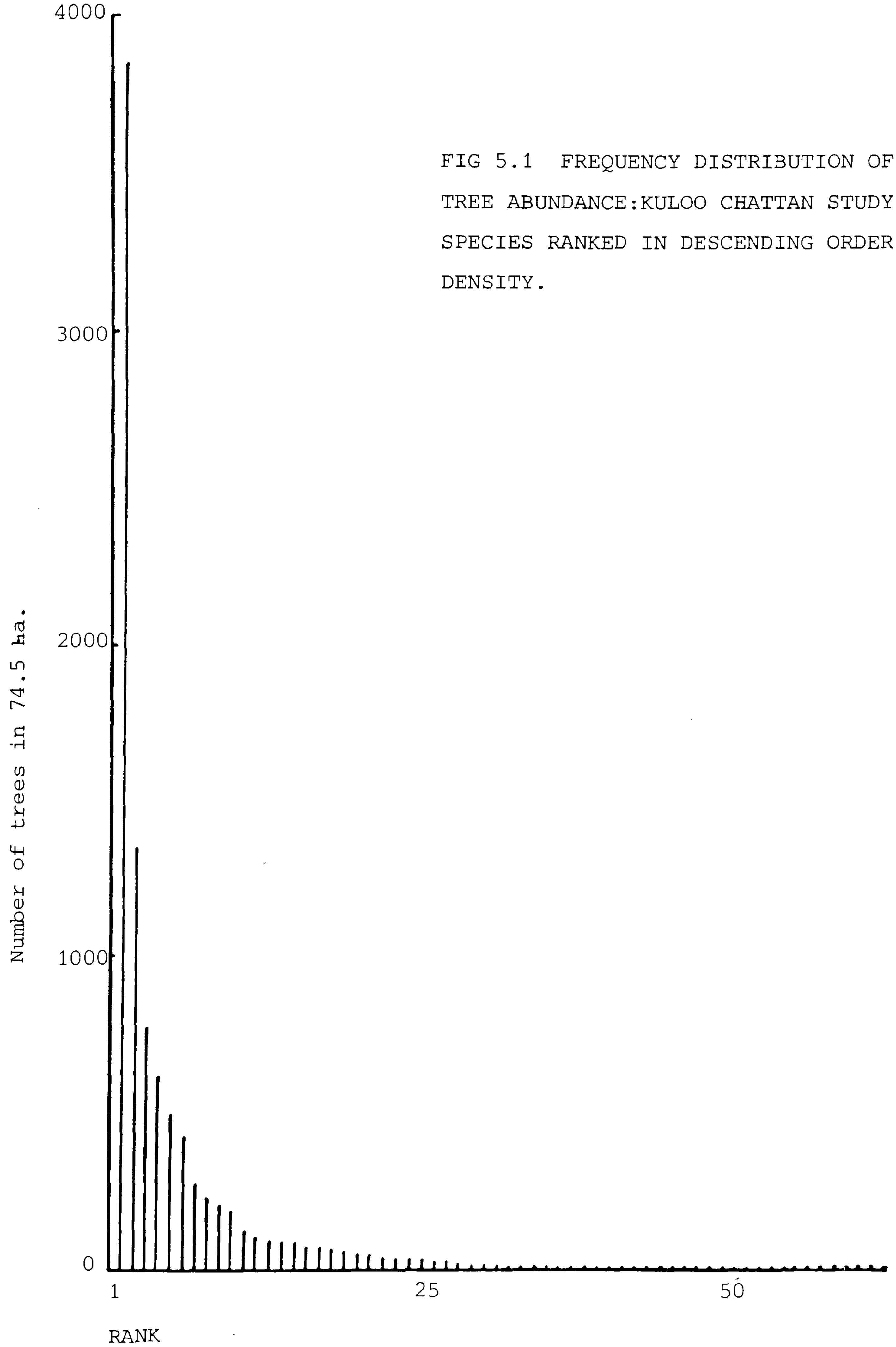


FIG 5.1 FREQUENCY DISTRIBUTION OF TREE TREE ABUNDANCE:KULOO CHATTAN STUDY AREA. SPECIES RANKED IN DESCENDING ORDER OF DENSITY.

FIG 5.2 SPECIES-AREA CURVE FOR TREE AND CLIMBER SPECIES.
KULOO CHATTAN STUDY SITE.

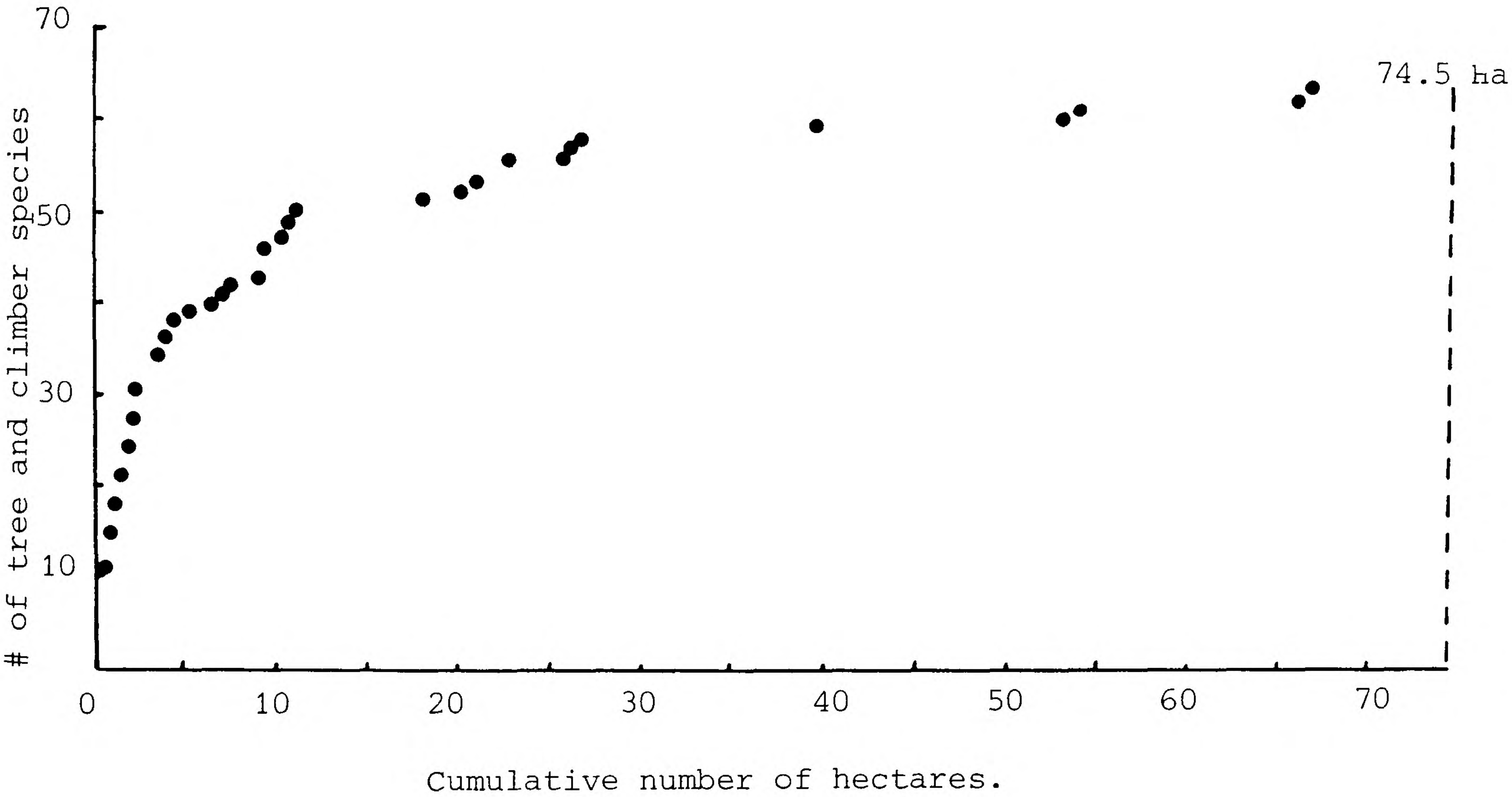


FIG 5.3 COMPARISON OF DOMINANCE AND DENSITY MEASURES FOR THE TOP TWENTY SPECIES DOMINANCE RANKS. (in descending order).
(see Table 5.A for details)

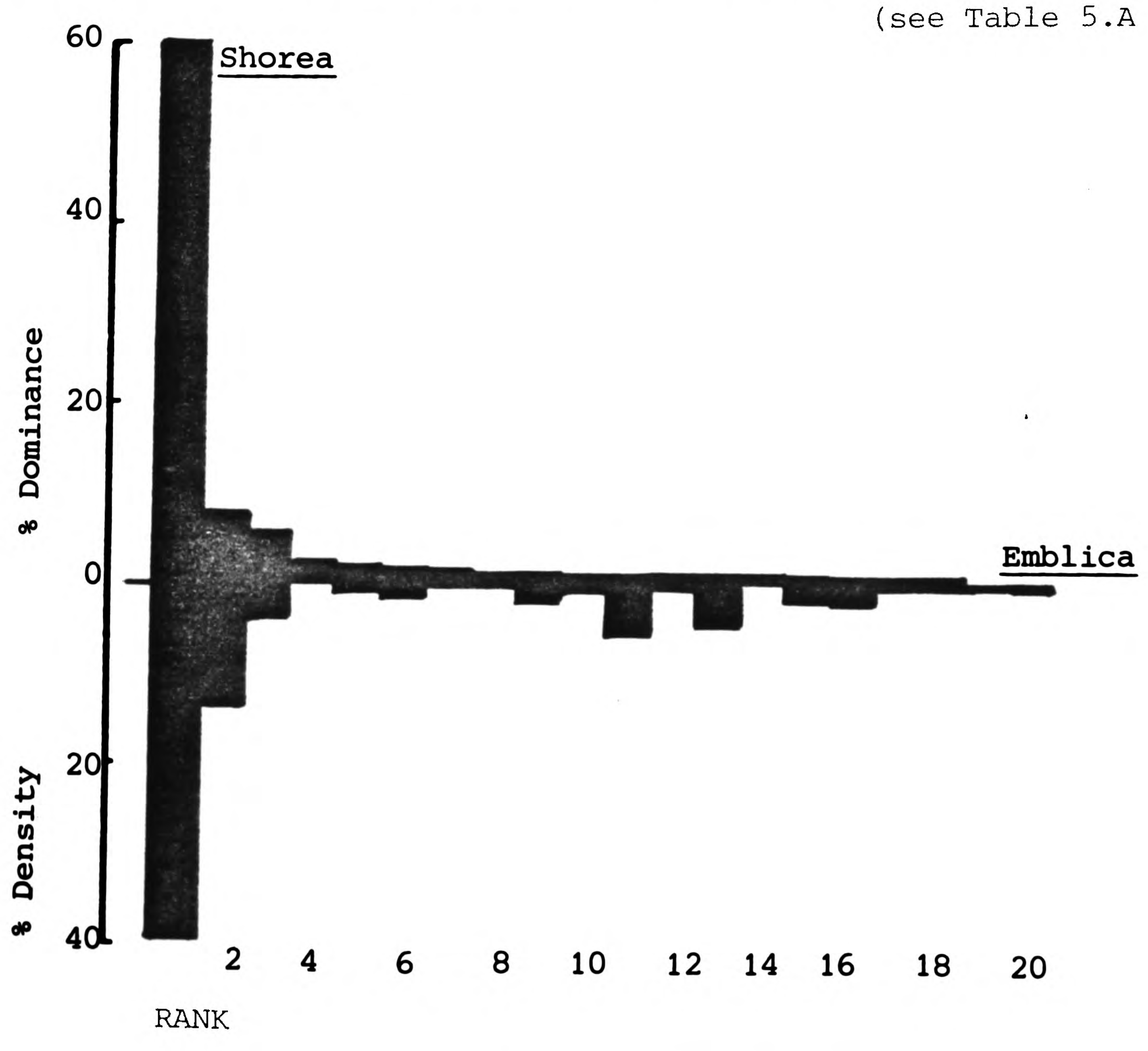
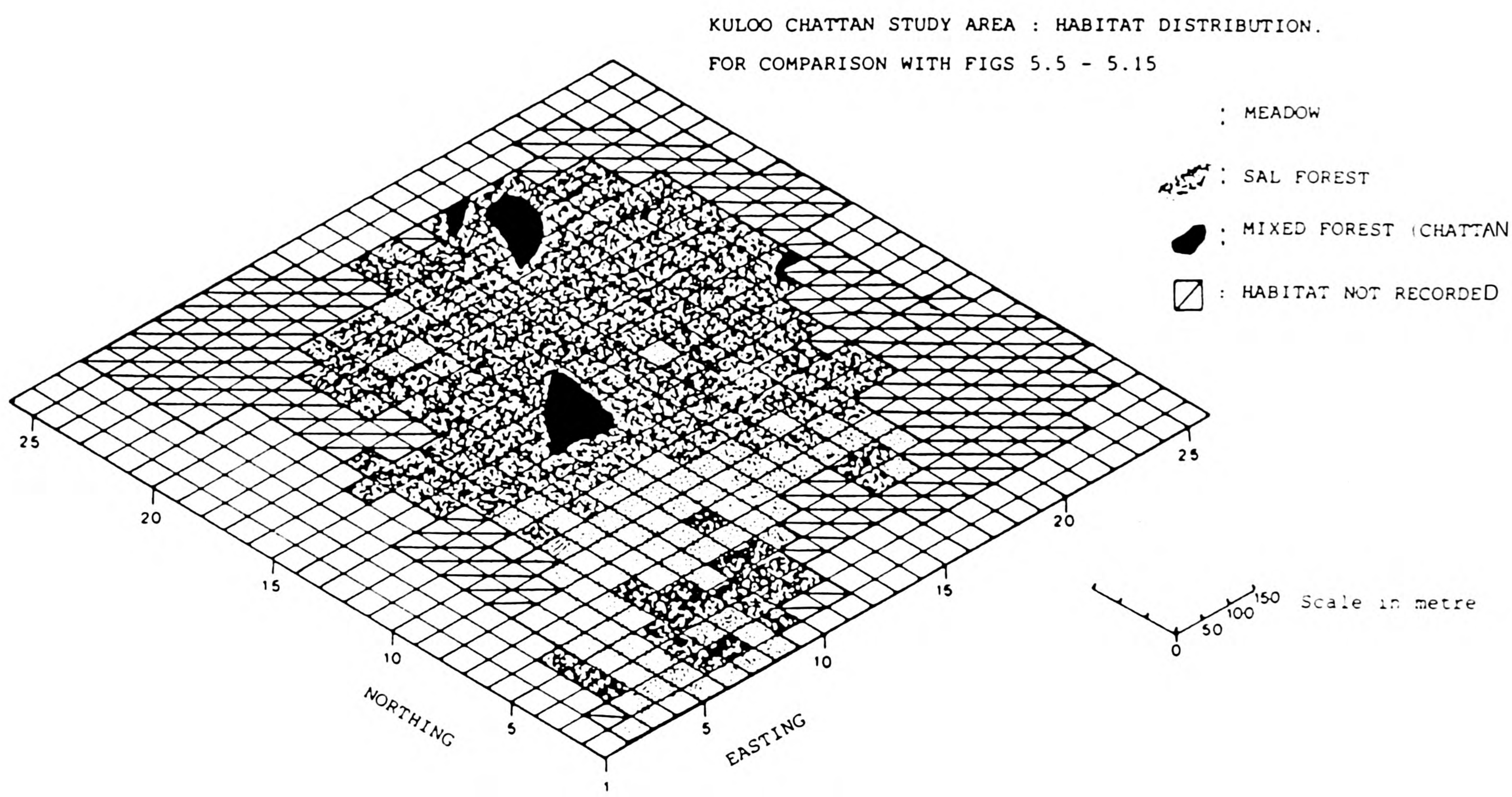


FIG 5.4 BASE MAP FOR FIGS 5.5-15 SHOWING HABITAT TYPES AND GRID SYSTEM.



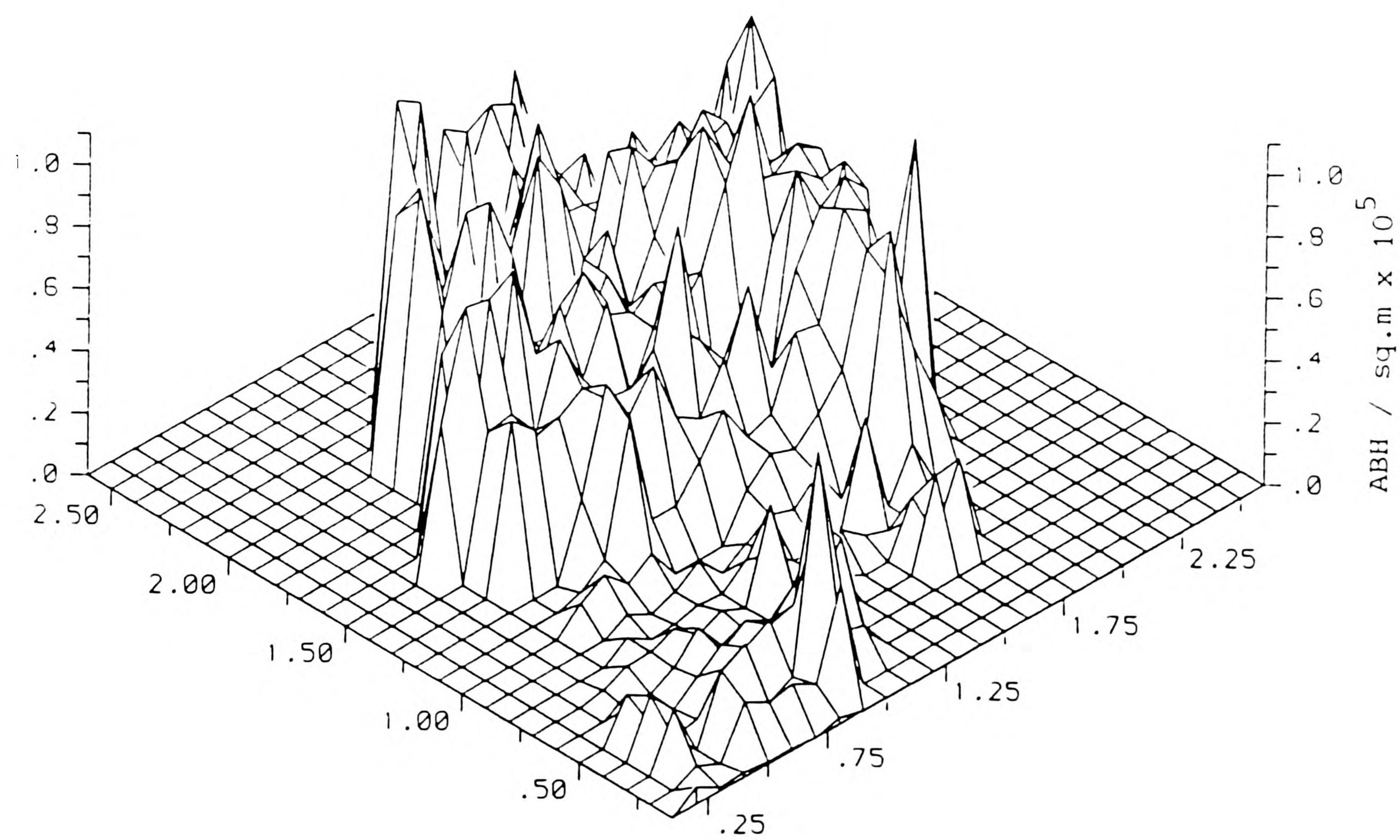


FIG 5.5 ALL TREES DOMINANCE DISTRIBUTION.

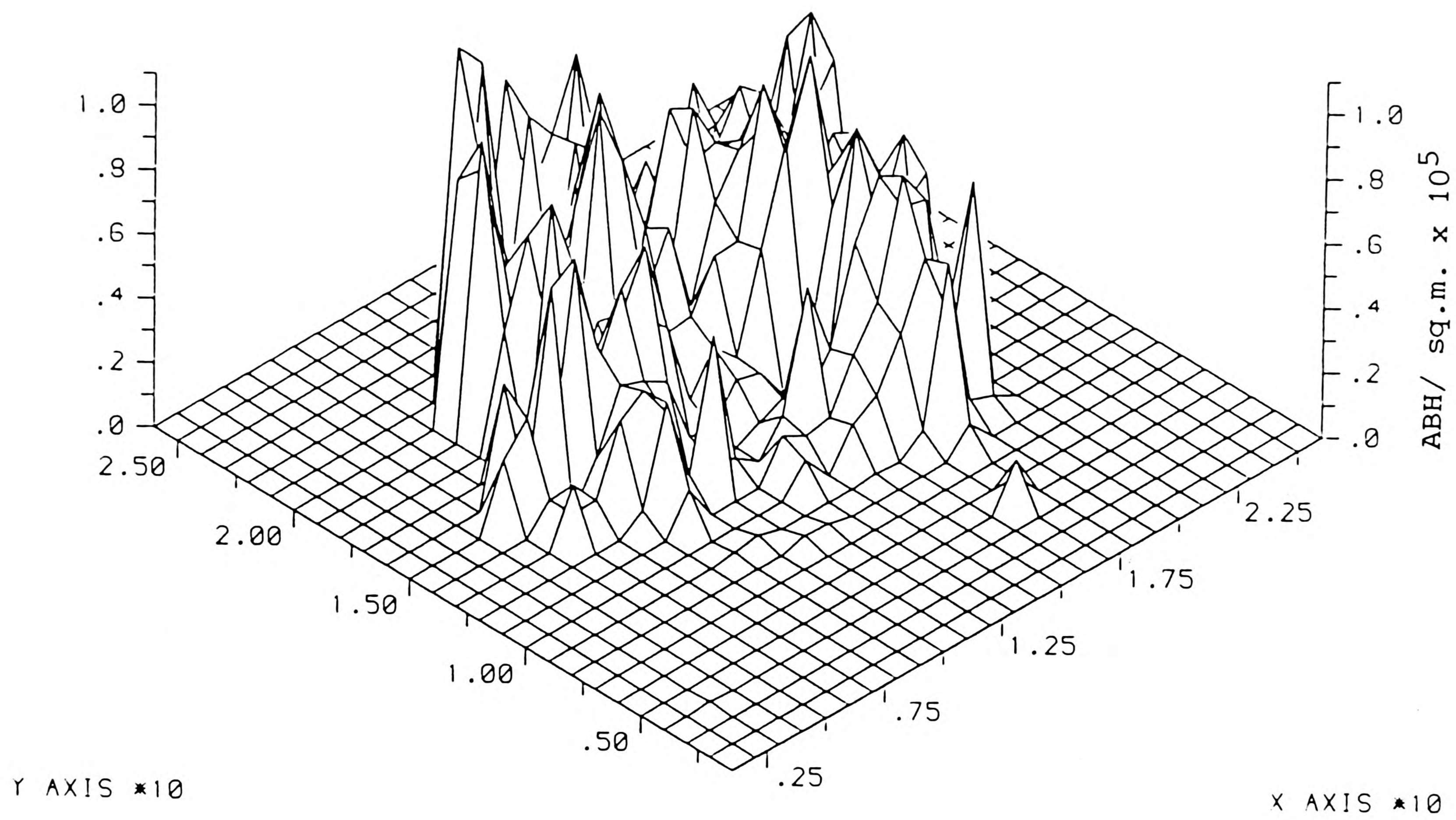


FIG 5.6 SHOREA ROBUSTA DOMINANCE DISTRIBUTION.

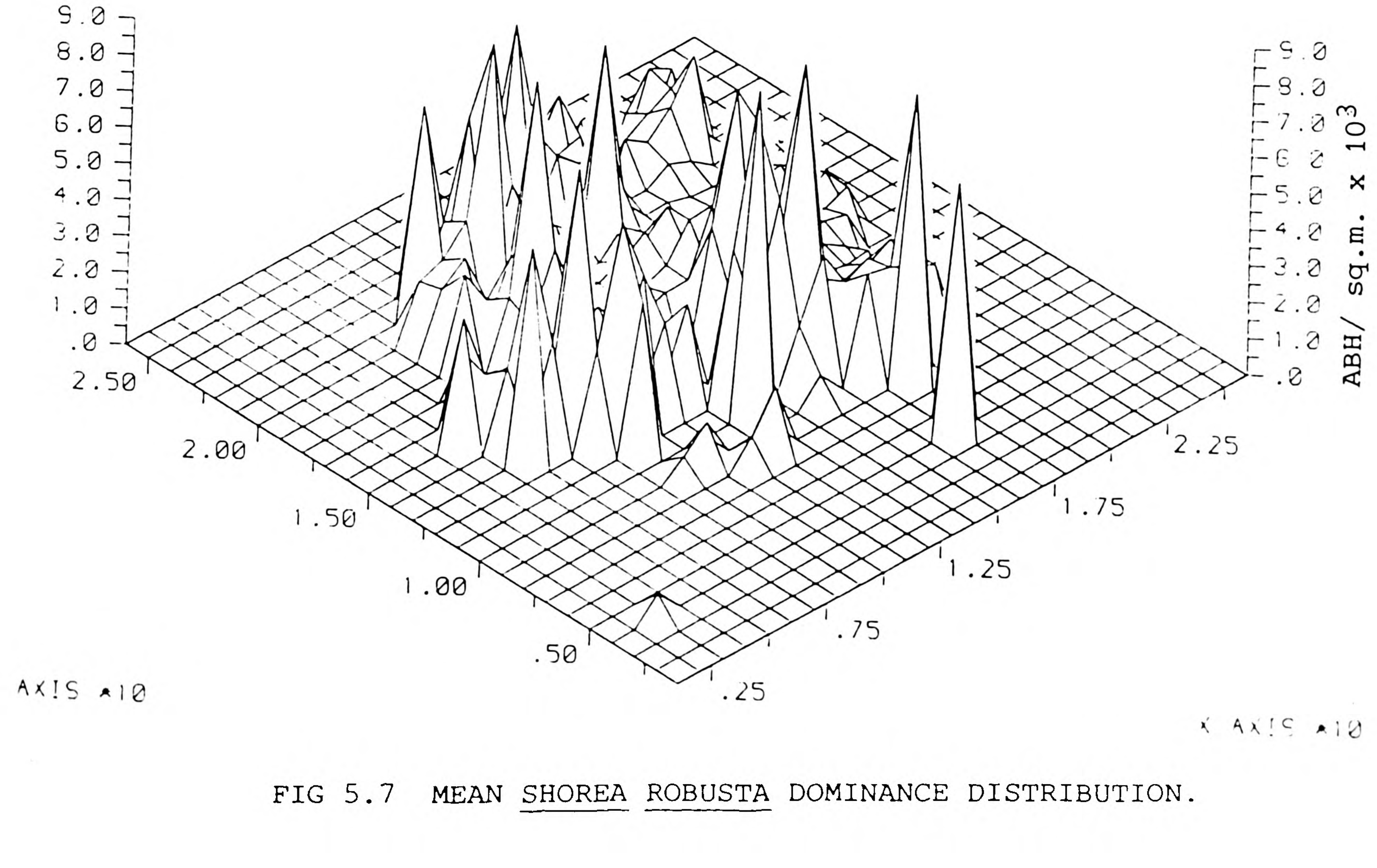


FIG 5.7 MEAN SHOREA ROBUSTA DOMINANCE DISTRIBUTION.

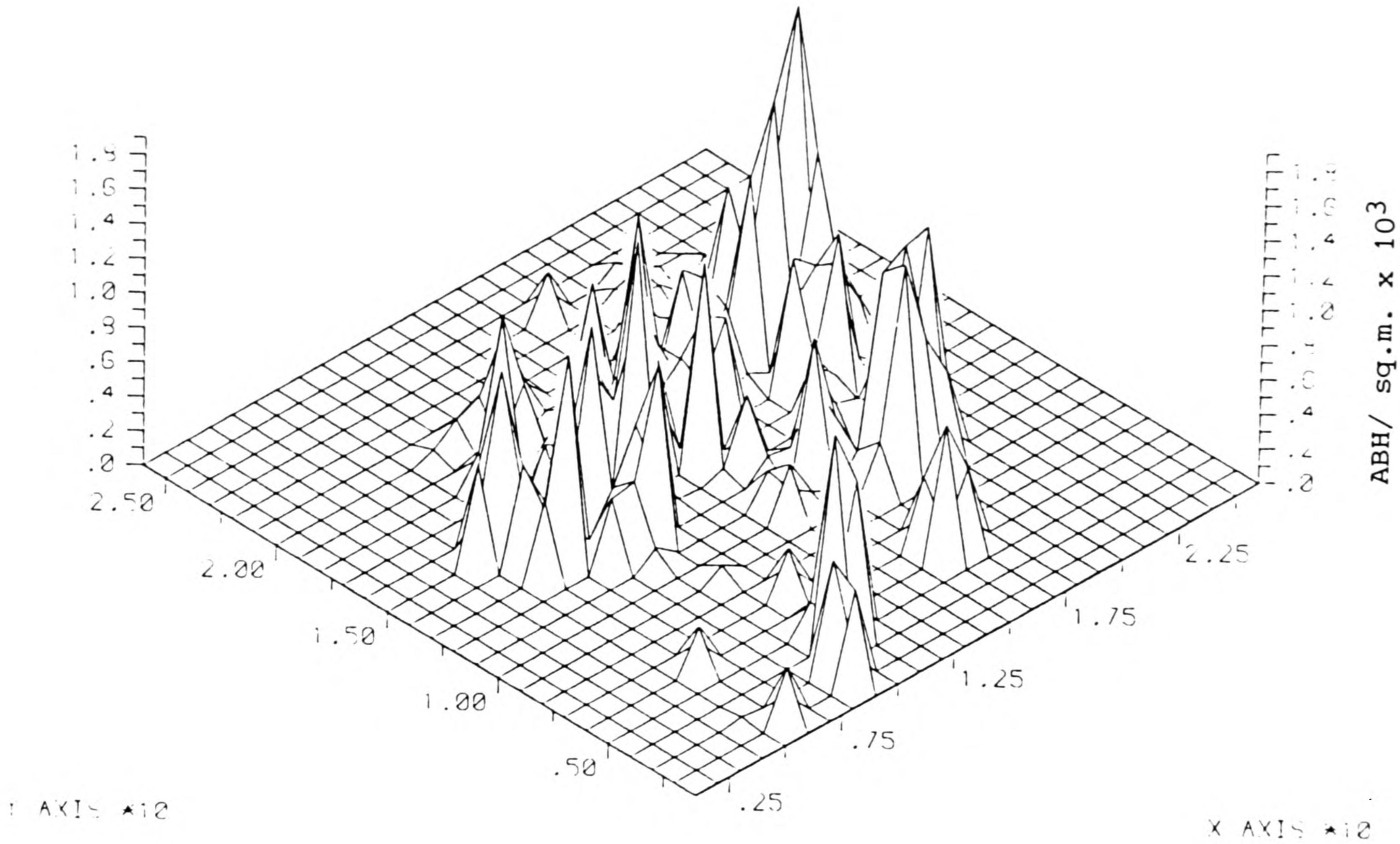


FIG 5.8 SYZGIUM CUMINI DOMINANCE DISTRIBUTION.

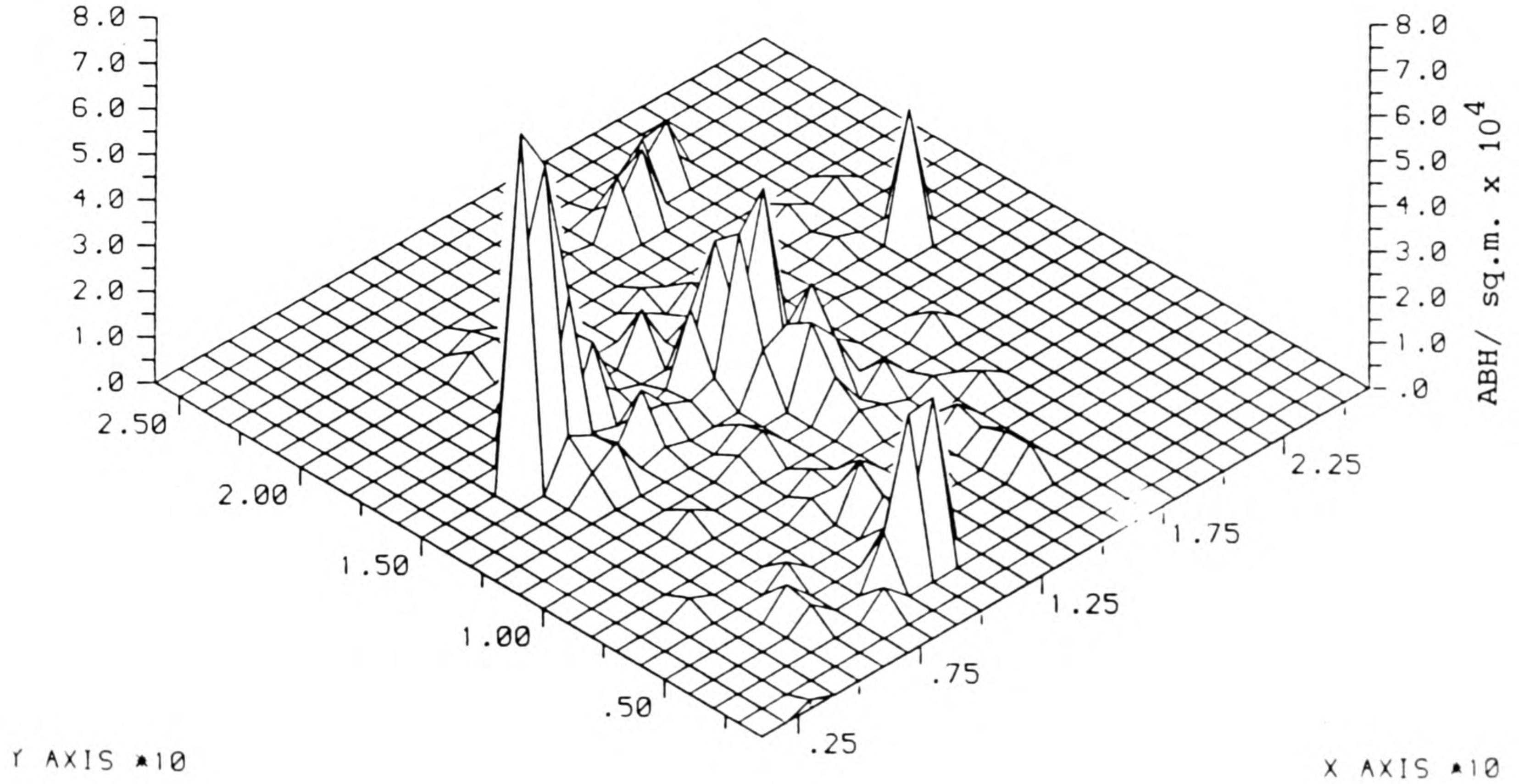


FIG 5.9 SACCOPETALUM TOMENTOSUM DOMINANCE DISTRIBUTION.

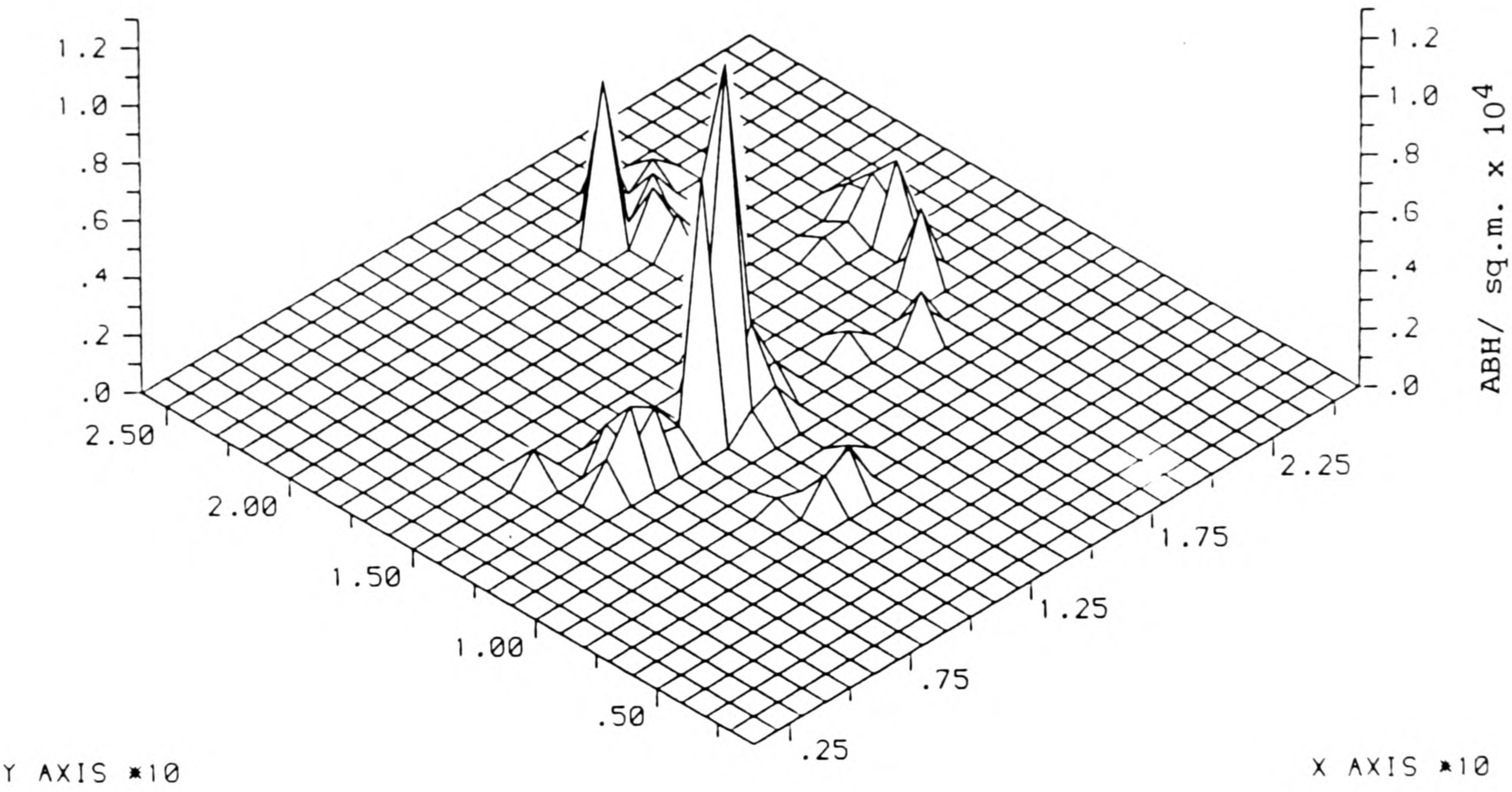


FIG 5.10 LANNEA CORAMANDELICA DOMINANCE DISTRIBUTION.

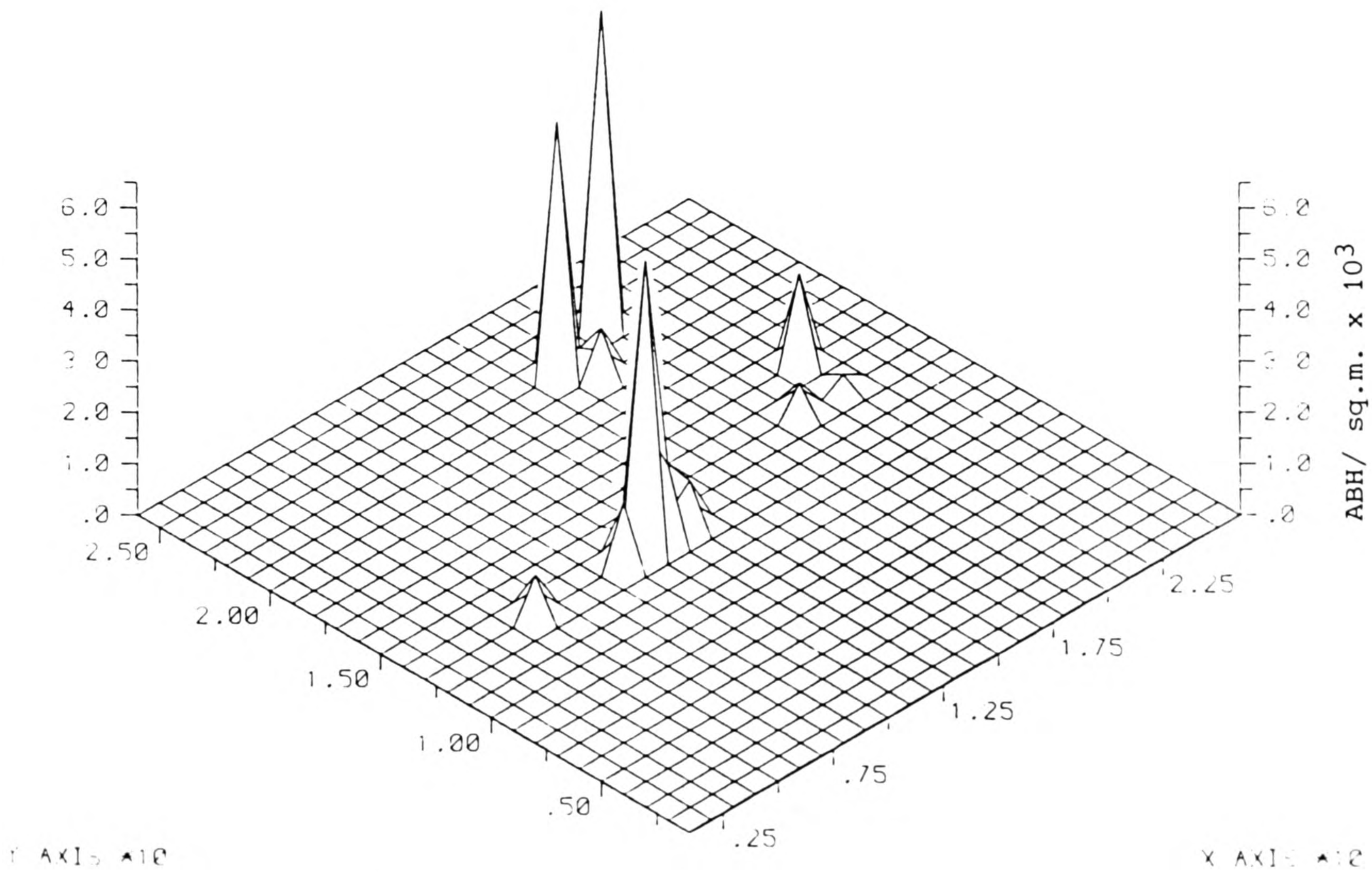


FIG 5.11 SCHLEICHERA OLEOSA DOMINANCE DISTRIBUTION.

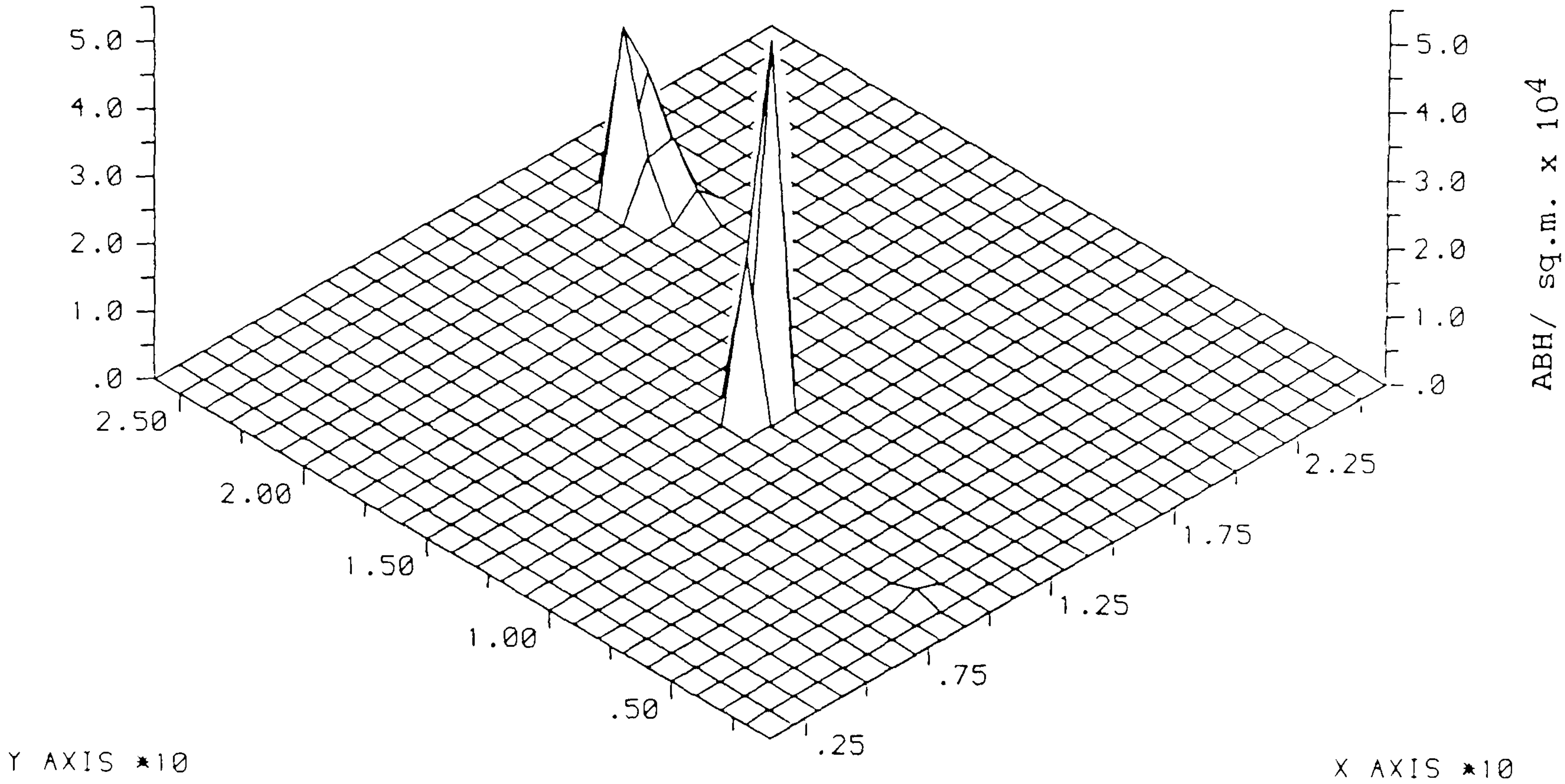


FIG 5.12 <u>FICUS TOMENTOSA</u> DOMINANCE DISTRIBUTION.

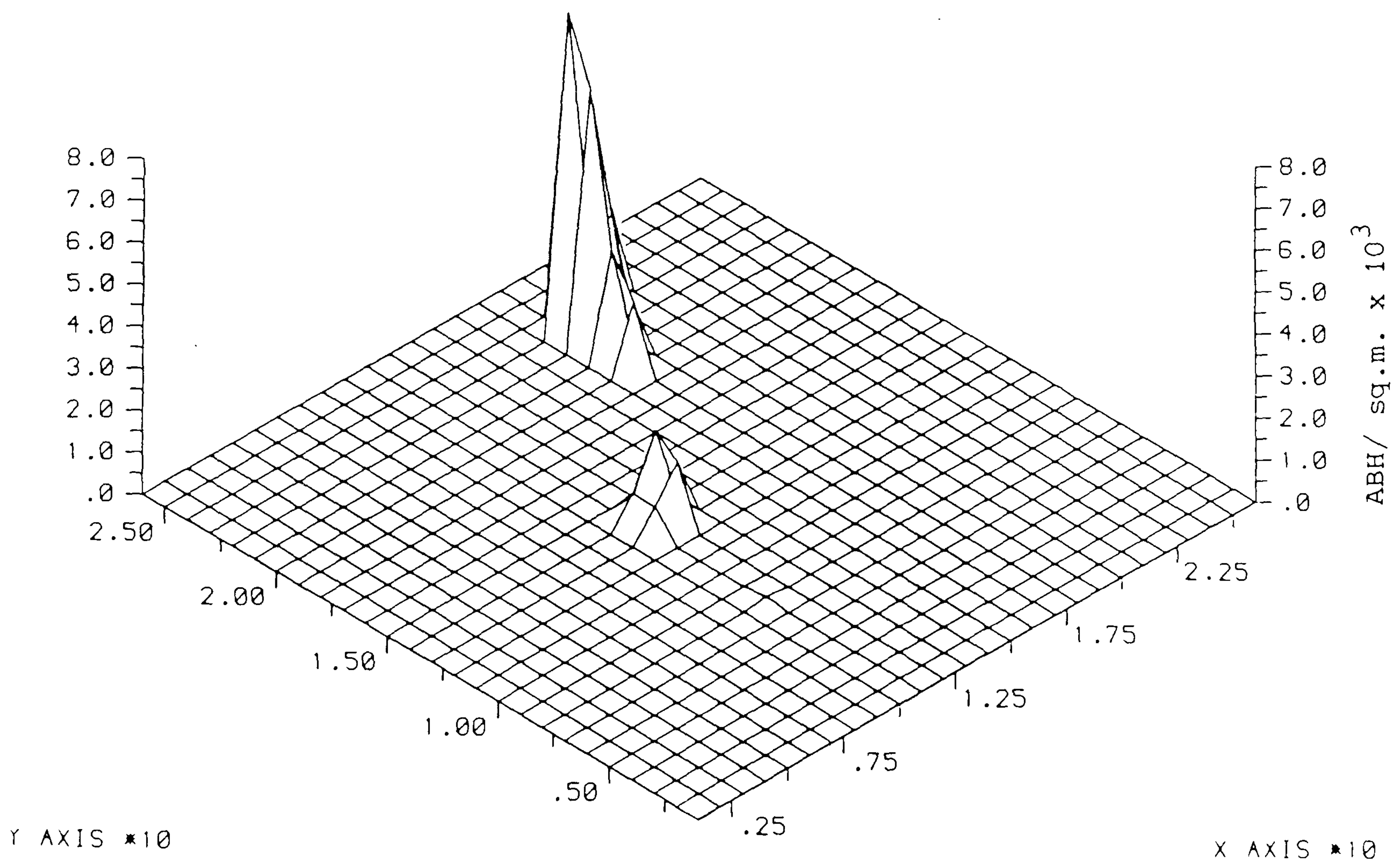


FIG 5.13 <u>STERCULIA URENS</u> DOMINANCE DISTRIBUTION.

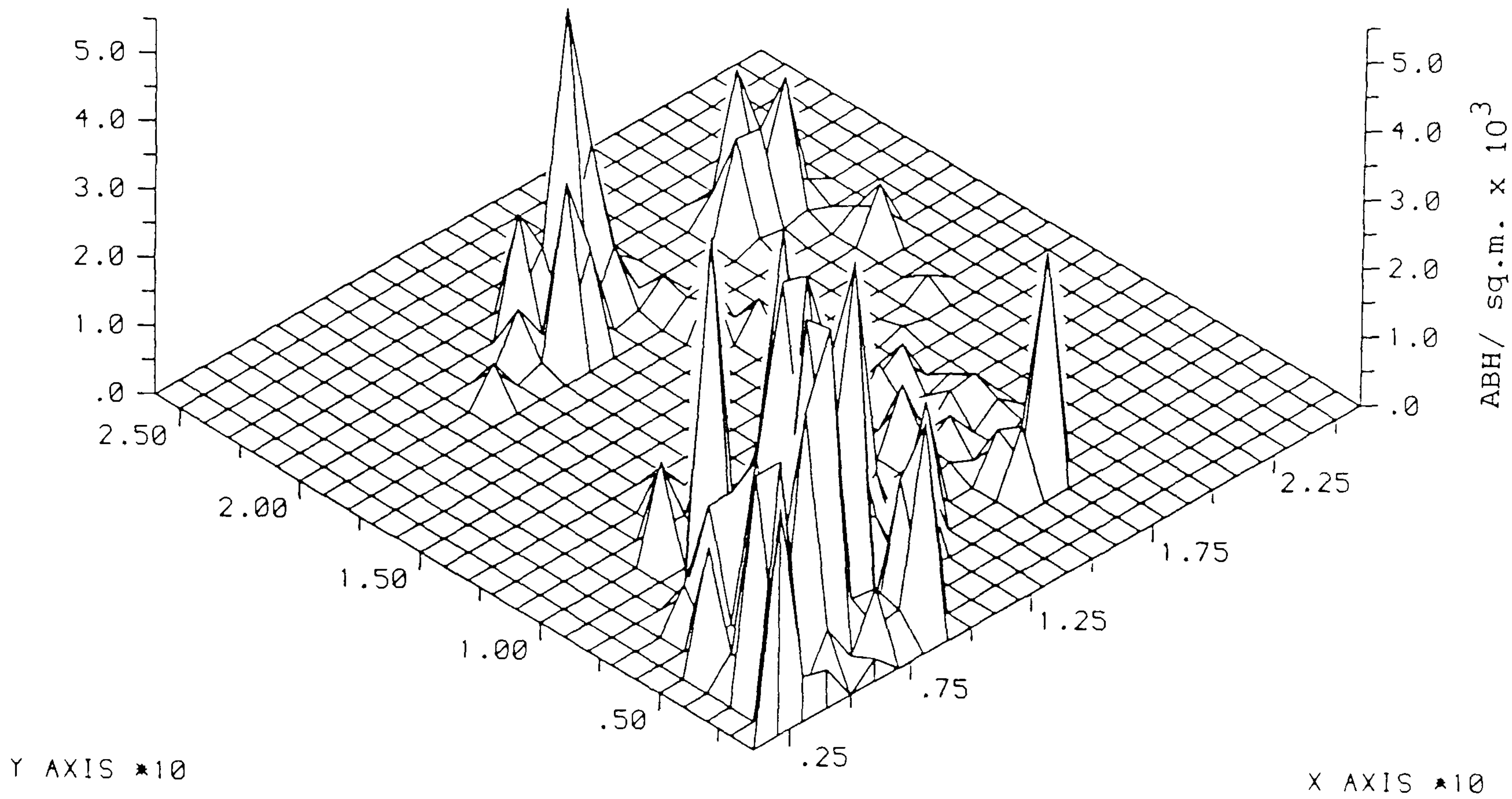


FIG 5.14 BUTEA MONOSPERMA DOMINANCE DISTRIBUTION.

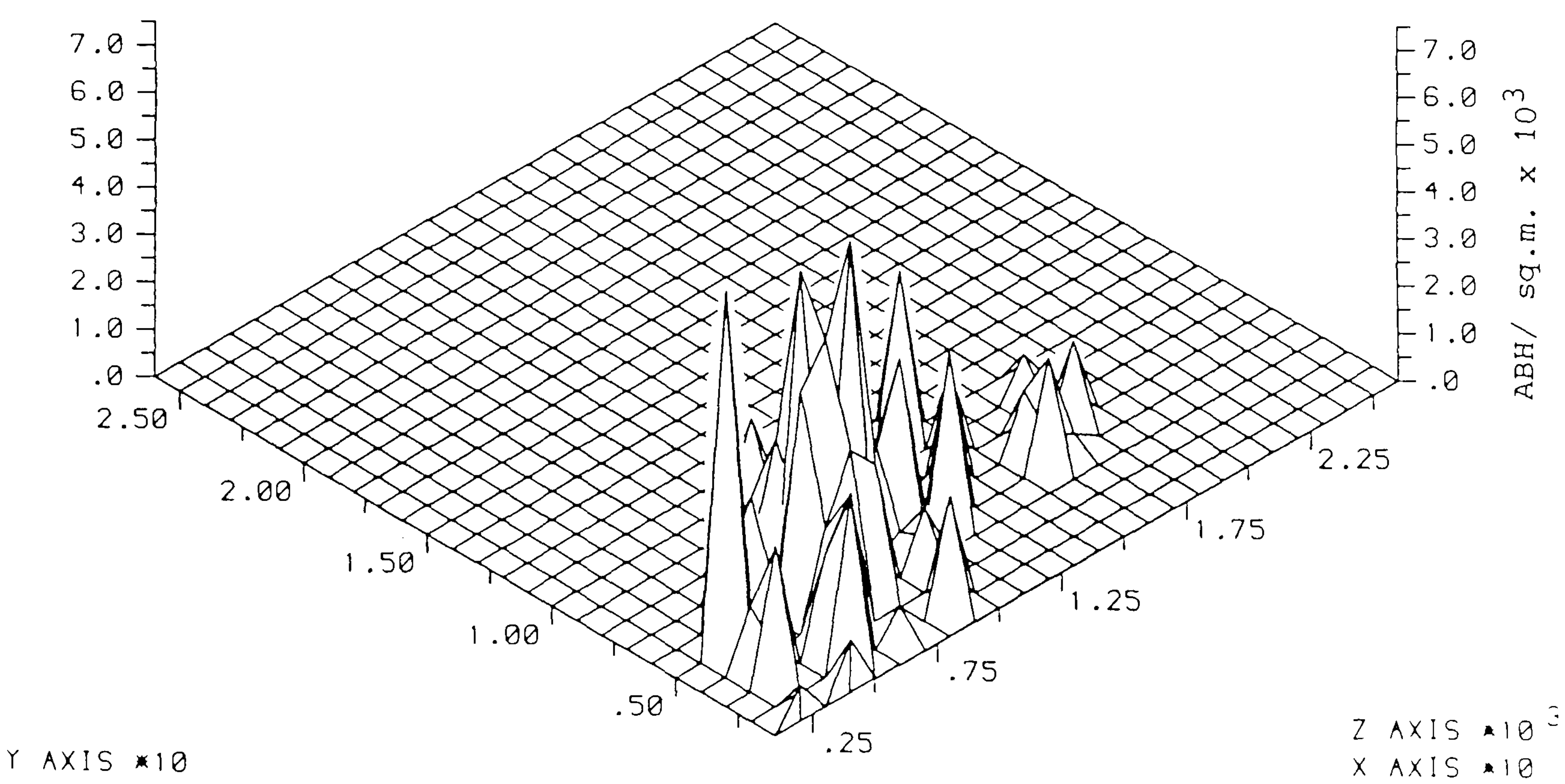


FIG 5.15 BOMBAX CEIBA DOMINANCE DISTRIBUTION.

KEY TO FIG 5.16, 5.17

◆ : FOLIAR ITEMS

Mature leaf	———
Young leaf	— — —
Open leaf bud	- - - - -
Leaf bud	....

● : REPRODUCTIVE ITEMS

Fruit	———
Flower	- - - -
Flowerbud	....

FIG 5.16 MONTHLY VARIATION IN MEAN PHENOLOGICAL SCORE FOR FOUR TREE SPECIES, FOR EACH PHYTOPHASE (see facing page for key)

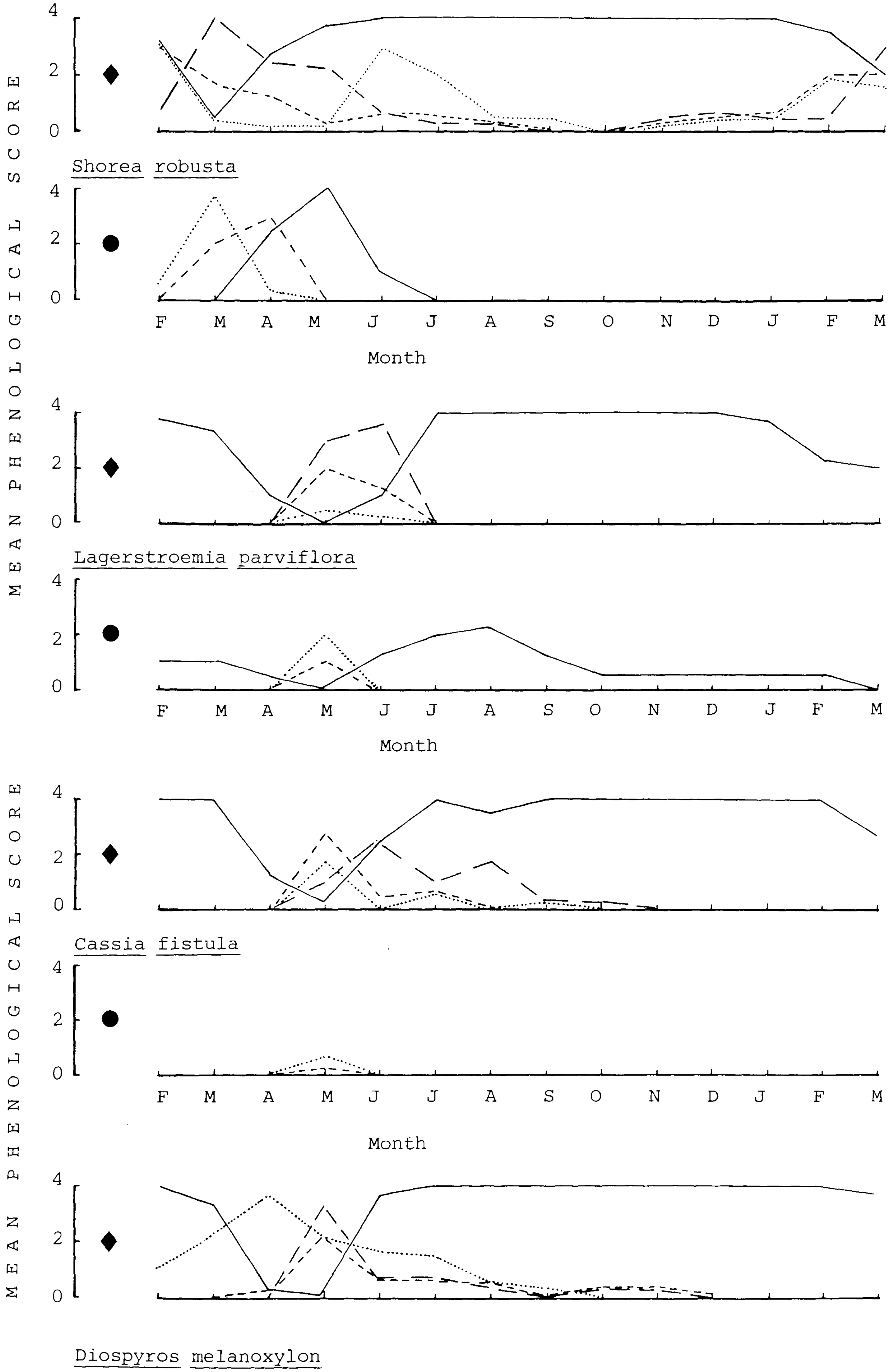


FIG 5.17 MONTHLY VARIATION IN TREE PHENOLOGICAL SCORE (see Fig 5.16)

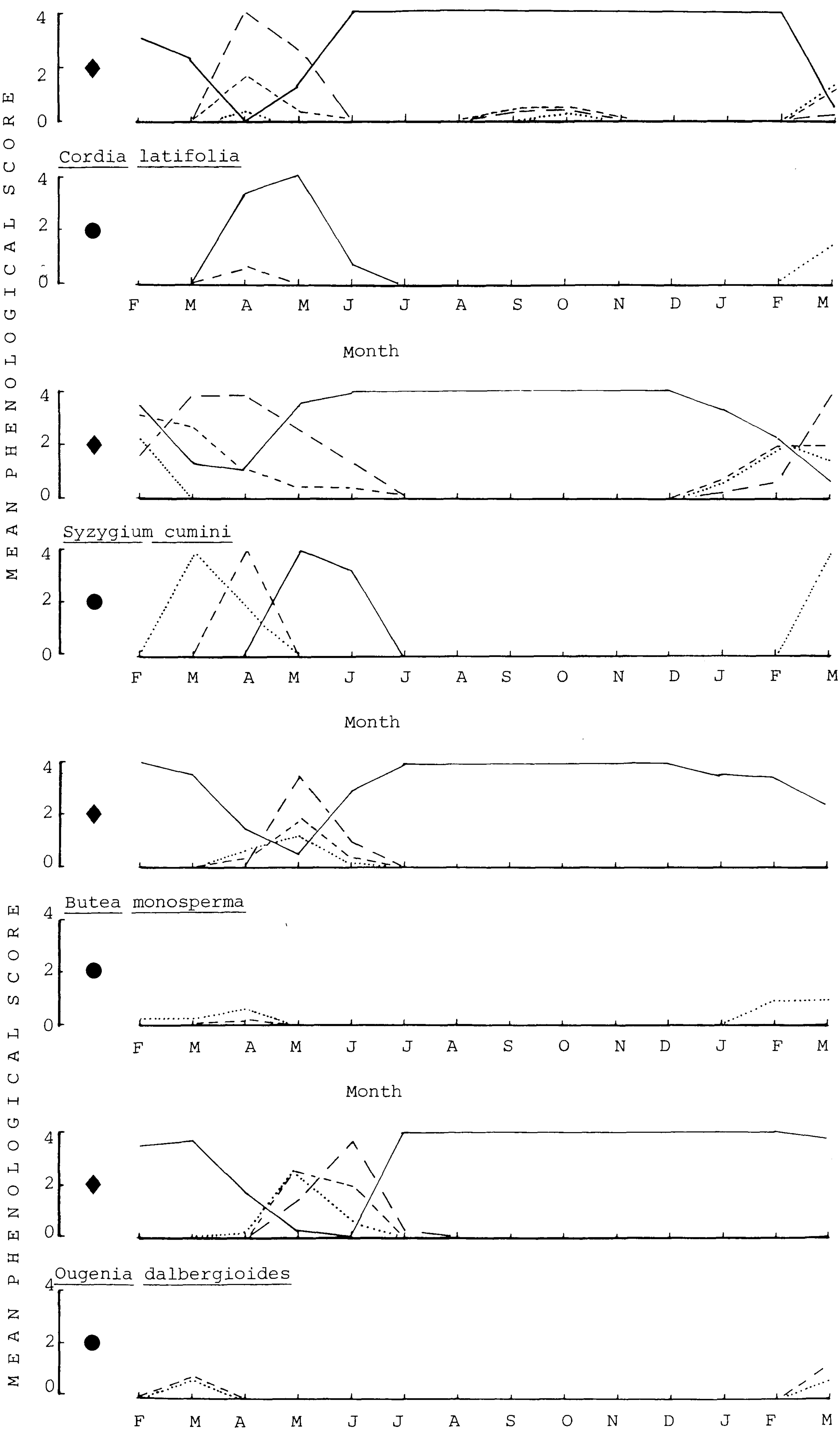


FIG 5.18 SEASONAL VARIATION IN PHENOLOGICAL AVAILABILITY INDEX.
FOR 49 TREE AND CLIMBER SPECIES.
FOR SEVEN PHYTOPHASES

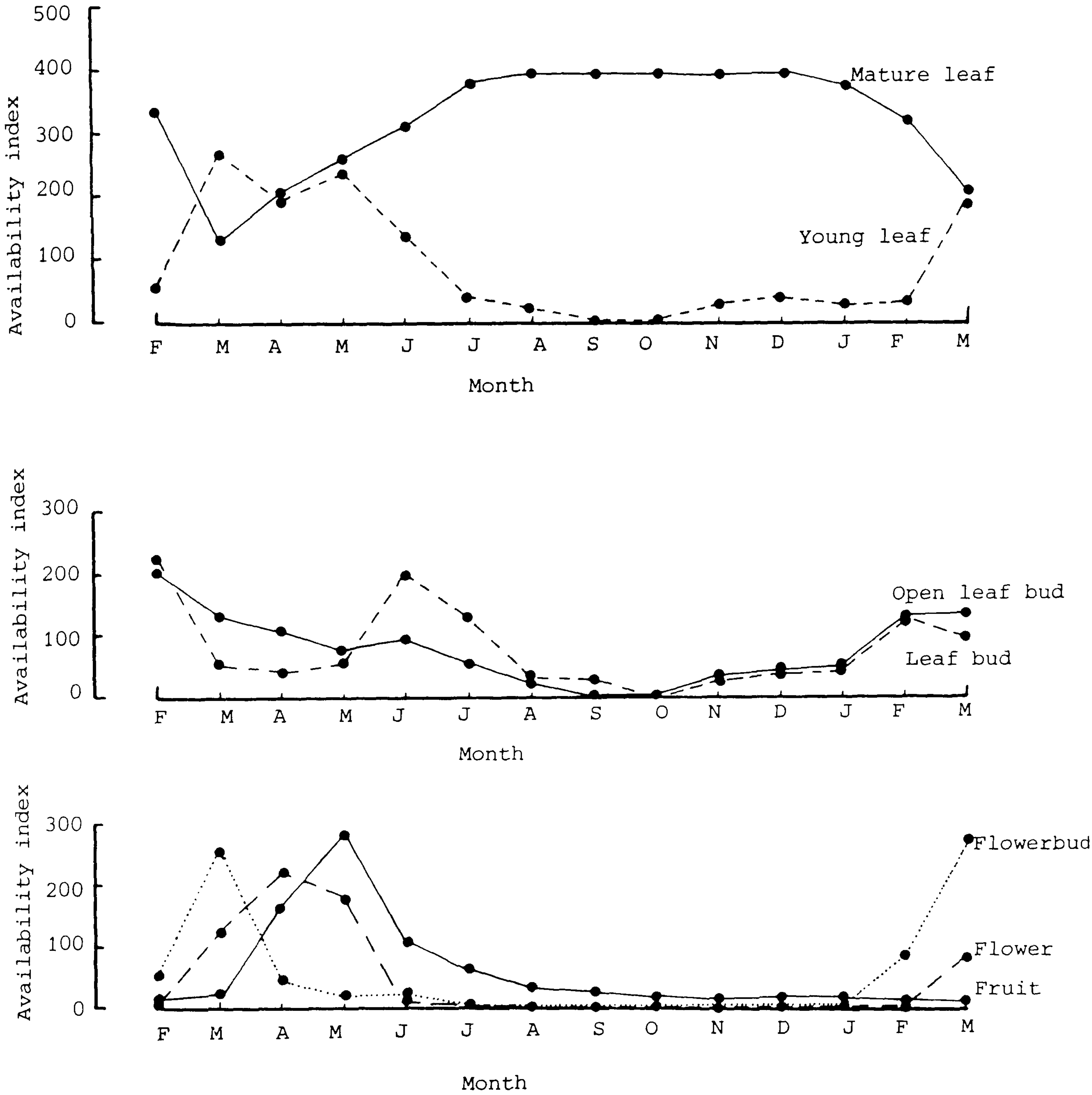


FIG 5.19 SEASONAL VARIATION IN PHENOLOGICAL AVAILABILITY INDEX.
FOR 48 TREE AND CLIMBER SPECIES,EXCLUDING *Shorea robusta*.
FOR SEVEN PHYTOPHASES.

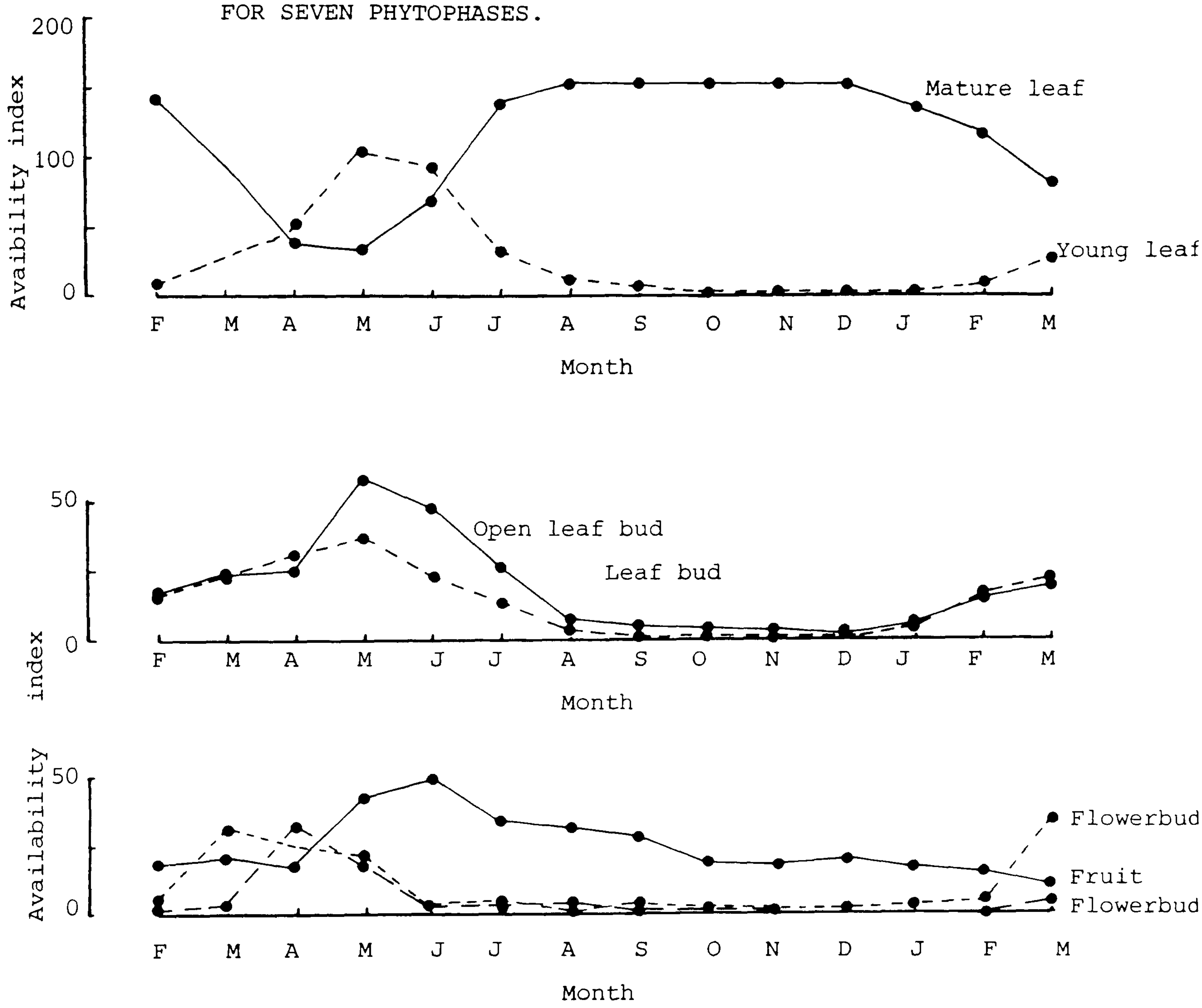


TABLE 5.A : MEASURES OF TREE ABUNDANCE AND DISPERSION.KULOO CHATTAN STUDY SITE. N= 9935 in 74.5 ha.
Species ranked in descending order of Dominance (see end of table for abbreviations).

	DOMINACE			DENSITY				FREQUENCY			IMPORTANCE VALUE		V/M RATIO
TREE SPECIES	RANK	ABH/m^2	RelD%	RANK	No.	Den/ha.	RelDen%	RANK	Freq	RelF%	RANK	IVI	
Shorea robusta	1	627.73	60.45	1	3878	13.013	39.0	3	177	7.72	1	107.17	26.24
Lagerstroemia parviflora	2	86.24	8.31	2	1350	4.530	13.6	1	219	9.55	2	31.46	17.11*
Syzygium cumini	3	59.33	5.71	6	431	1.446	4.3	5	140	6.10	4	16.11	4.26*
Ficus infectoria	4	28.37	2.73	27	27	0.091	0.3	21	27	1.18	14	4.21	0.91+
Terminalia chebula	5	17.48	1.68	11	119	0.400	1.2	8	75	3.27	10	6.15	2.12*
Butea monosperma	6	14.92	1.44	7	277	0.929	2.8	7	117	5.11	8	9.35	3.34*
Ficus tomentosa	7	14.24	1.37	38	11	0.037	0.1	33	8	0.35	5	14.69	–
Pterocarpus marsupium	8	12.39	1.19	22	38	0.128	0.4	18	33	1.44	18	3.03	1.14*
Ougenia dalbergioides	9	12.38	1.19	8	221	0.742	2.2	10	60	2.48	11	5.87	6.03*
Stereospermum suaveolens	10	11.36	1.09	13	93	0.312	0.9	11	58	2.53	13	4.52	1.77*
Diospyros melanoxylon	11	10.63	1.02	4	602	2.020	6.1	6	139	6.06	6	13.18	7.92*
Bombax ceiba	12	10.58	1.02	17	73	0.245	0.7	14	47	2.05	16	3.77	1.83*
Cordia latifolia	13	10.40	1.00	5	496	1.664	5.0	4	152	6.63	7	12.63	4.36*
Terminalia balerica	14	9.52	0.92	32	19	0.064	0.2	25	19	0.83	25	1.95	0.94+
Mallotus philippensis	15	9.35	0.90	10	187	0.628	1.9	9	69	2.83	12	5.63	5.17*
Saccopetalum tomentosum	16	8.92	0.86	9	216	0.725	2.2	7	93	4.00	9	7.06	6.79*
Adina cordifolia	17	7.89	0.76	33	18	0.060	0.2	30	13	0.57	31	1.53	1.62*
Lannea coramandelica	18	6.65	0.64	18	55	0.185	0.6	18	33	1.44	21	2.68	3.18*
Terminalia tomentosa	19	6.00	0.58	21	43	0.144	0.4	19	30	1.31	23	2.29	1.66*
Emblica officinalis	20	5.93	0.57	16	79	0.265	0.8	13	49	2.13	17	3.50	2.08*
Bauhinia retusa	21	5.05	0.49	24	34	0.114	0.3	25	19	0.83	28	1.66	2.25*
Buchanania lanzan	22	4.49	0.48	14	89	0.298	0.9	12	57	2.48	15	3.86	1.76*
Tectona grandis	23	4.01	0.39	12	107	0.359	1.1	26	17	0.74	24	2.21	22.65*
Bauhinia malabarica	24	4.01	0.39	15	85	0.285	0.9	17	39	1.70	19	2.99	5.59*
Careya arborea	25	3.88	0.37	18	55	0.185	0.6	15	44	1.92	20	2.89	1.29*

TABLE 5.A (Contd.)

TREE SPECIES	DOMINACE			DENSITY				FREQUENCY			IMPORTANCE VALUE		V/M RATIO
	RANK	ABH/m^2	RelD%	RANK	No.	Den/ha.	RelDen%	RANK	Freq	RelF%	RANK	IVI	
Gardenia latifolia	26	3.87	0.37	23	37	0.124	0.4	22	26	1.13	26	1.90	1.91*
Cassia fistula	27	3.49	0.34	3	809	2.715	8.1	2	194	8.42	3	16.86	8.54*
Ficus arnottiana	28	3.35	0.32	37	13	0.044	0.1	35	6	0.26	43	0.68	–
Bridelia retusa	29	3.15	0.30	25	32	0.107	0.3	23	23	1.00	29	1.60	2.09*
Sterculia urens	30	2.95	0.28	29	24	0.080	0.2	31	12	0.52	38	1.00	3.25*
Schleichera oleosa	31	2.83	0.27	31	20	0.067	0.2	28	15	0.65	34	1.12	2.04*
Ficus religiosa	32	2.60	0.25	40	8	0.027	0.1	33	8	0.35	41	0.70	–
Madhuca indica	33	2.41	0.23	24	34	0.114	0.3	22	26	1.13	28	1.66	1.36*
Anogeissus latifolia	34	2.28	0.22	33	18	0.060	0.2	29	14	0.61	37	1.03	1.40*
Albizzia odoratissima	35	2.26	0.22	35	15	0.050	0.2	28	15	0.65	36	1.07	0.96+
Bauhinia racemosa	36	2.23	0.21	20	52	0.175	0.5	16	42	1.83	22	2.54	1.45*
Semecarpus anacardium	37	1.98	0.19	28	25	0.084	0.3	24	22	0.96	32	1.45	1.24*
Zizyphus xylopyra	38	1.84	0.18	22	38	0.128	0.4	20	28	1.22	27	1.80	1.60*
Litsea polyantha	39	1.42	0.14	30	22	0.074	0.2	30	13	0.57	40	0.91	2.84*
Grewia tilaefolia	40	1.42	0.14	36	14	0.047	0.1	32	11	0.48	42	0.72	1.53*
Mitragyna parviflora	41	1.35	0.13	43	3	0.010	0.03	36	3	0.13	46	0.29	–
Stereospermum xylocarpum	42	1.14	0.11	34	16	0.054	0.2	28	15	0.65	39	0.96	1.07+
Zizyphus jujuba	43	0.98	0.09	28	25	0.084	0.3	27	16	0.70	35	1.09	2.19*
Ehretia laevis	44	0.97	0.09	26	28	0.094	0.3	25	19	0.83	33	1.22	1.84*
Cordia myxa	45	0.86	0.08	19	53	0.178	0.5	23	23	1.00	30	1.58	3.85*
Ficus glomerata	46	0.67	0.06	45	1	0.003	0.01	38	1	0.05	51	0.12	–
Glochidion velutinum	47	0.52	0.05	39	10	0.034	0.1	35	6	0.26	45	0.41	–
Litsea sebifera	48	0.49	0.05	42	6	0.020	0.1	38	1	0.05	49	0.15	–
Holopetala integrifolia	49	0.45	0.04	45	1	0.003	0.01	38	1	0.05	54	0.07	–
Casearia tomentosa	50	0.31	0.03	43	3	0.010	0.03	36	3	0.13	47	0.19	–

TABLE 5.A (Contd.)

TREE SPECIES	DOMINACE			DENSITY				FREQUENCY			IMPORTANCE VALUE		V/M RATIO
	RANK	ABH/m^2	RelD%	RANK	No.	Den/ha.	RelDen%	RANK	Freq	RelF%	RANK	IVI	
Dalbergia paniculata	51	0.22	0.02	43	3	0.010	0.03	36	3	0.13	48	0.18	–
Erythrina suberosa	52	0.16	0.02	44	2	0.007	0.02	37	2	0.09	50	0.13	–
Ficus cunia	52	0.16	0.02	45	1	0.003	0.01	38	1	0.05	53	0.08	–
Cordia macleodii	53	0.06	0.005	44	2	0.007	0.02	37	2	0.09	44	0.14	–
Embelia robusta	54	0.05	0.005	41	7	0.023	0.1	34	7	0.30	45	0.41	–
Flacourtia ramontchi	55	0.05	0.005	44	2	0.007	0.02	38	1	0.05	53	0.08	–
Garuga pinnata	56	0.04	0.004	45	1	0.003	0.01	38	1	0.05	55	0.06	–
Kydia calycina	57	0.03	0.003	45	1	0.003	0.01	38	1	0.05	55	0.06	–
Herbarium Sp.No 256	58	0.01	0.001	45	1	0.003	0.01	38	1	0.05	55	0.06	–
Casearia graveolens	59	0.009	0.001	44	1	0.003	0.01	37	2	0.09	52	0.10	–
Randia dumentorum	60	0.006	0.001	45	1	0.003	0.01	38	1	0.05	55	0.06	–
Specimen in Q 16/05	61	0.005	0.001	45	1	0.003	0.01	38	1	0.05	55	0.06	–

For definitions see text.

Abbreviations :

- ABH/m^2 = Tree cross-sectional area at breast height in m^2.
- RelD% = Relative Dominance.
- No = Number.
- Den/Ha = Number of individual trees per hectare.
- RelDen% = Relative Density.
- Freq = Frequency of species in 0.25 ha quadrats.
- RelF% = Relative Frequency.
- IVI = Importance Value Index.
- V/M Ratio = Variance:Mean Ratio.
- * = Departure of V/M ratio from 1 significant at $P < 0.001$.
- + = Departure of V/M ratio from 1 not significant at $P > 0.001$.

TABLE 5.B MEASURES OF ABUNDANCE:KULOO CHATTAN STUDY SITE. BY TREE FAMILIES. N= 9935 in 74.5 ha.

	Number of		Dominance			Density	
Family	Spp.	Trees	Rank	ABH/m^2	RelD%	Rank	RelDen%
DIPTEROCARPACEAE	1	3878	1	627.73	60.45	1	39.03
LYTHRACEAE	2	1351	2	86.24	8.31	2	13.60
MYRTACEAE	2	486	3	63.21	6.08	7	4.89
MORACEAE	6	61	4	49.39	4.75	16	0.61
PAPILIONACEAE	5	541	5	40.07	3.86	6	5.44
COMBRETACEAE	4	199	6	35.28	3.40	10	2.00
EUPHORBIACEAE	4	308	7	18.95	1.82	8	3.10
CAESALPINIACEAE	4	980	8	14.78	1.43	3	9.86
ANACARDIACEAE	3	169	9	13.12	1.26	11	1.70
RUBIACEAE	4	59	9	13.12	1.26	17	0.70
BIGNONIACEAE	2	109	10	12.50	1.20	12	1.09
EHRETIACEAE	4	579	11	12.29	1.18	5	5.83
EBENACEAE	1	602	12	10.63	1.02	4	6.06
BOMBACEAE	1	73	13	10.58	1.02	14	0.74
ANONACEAE	1	216	14	8.92	0.86	9	2.17
VERBENACEAE	1	107	15	4.01	0.39	13	1.08
STERCULIACEAE	1	24	16	2.95	0.28	20	0.24
SAPINDACEAE	1	20	17	2.83	0.27	21	0.20
RHAMNACEAE	2	63	18	2.82	0.27	15	0.63
SAPOTACEAE	1	34	19	2.41	0.23	18	0.34
MIMOSACEAE	1	15	20	2.26	0.22	22	0.15
LAURACEAE	2	28	21	1.91	0.19	19	0.28
TILIACEAE	1	14	22	1.42	0.14	23	0.14
ULMACEAE	1	1	23	0.45	0.04	25	0.01
FLACOURTIACEAE	3	7	24	0.37	0.04	24	0.07
MYRSINACEAE	1	7	25	0.03	0.005	24	0.07
MALVACEAE	1	1	26	0.03	0.003	25	0.01
BURSERACEAE	1	1	27	0.03	0.003	25	0.01
Unknown affinity	2	2	20	2.26	0.22	22	0.15
LAURACEAE	2	28	21	1.91	0.19	19	0.28

CHAPTER 6

LANGUR SOCIAL ORGANISATION AND INFANTICIDE

CHAPTER 6 LANGUR SOCIAL ORGANISATION AND INFANTICIDE.

6.1 INTRODUCTION.

Hanuman langurs show considerable variation in the pattern and stability of the membership of social groups. As noted in Chapter 4, most mature males aggregate into 'bachelor' bands whilst females remain in the natal group with one or a few adult males whose residency is unstable. Troops split, merge, are created and dissolved. One of the most frequent social changes is the replacement of the adult male of a unimale troop by an extra-troop male. At three sites published accounts describe male takeovers, associated with infant disappearance and occasionally with infanticide by the invading male. This infant killing has elicited considerable controversy (Hrdy 1977b).

In this chapter, firstly (6.3) the structure of the Kanha population is described and compared with that other sites. Hypotheses relating aspects of social organisation are considered. In the following section (6.4) data on langur reproduction and mortality is presented and discussed. The subsequent four sections are concerned with social change and infanticide. In 6.5 types of social change are categorized and reviewed from a range of published langur populations. In 6.6 hypotheses seeking to explain the occurrence of infanticide are reviewed and the evidence for and against them is discussed. In 6.7 observations from Kanha of social change and infanticide are presented and discussed with reference to other published accounts and the hypotheses considered in 6.6. In 6.8, the concluding discussion, aspects of infanticide in langurs, and mammals generally, are considered. Individual animals are referred to using the abbreviations given in Table 4.A and superscript numbers (e.g. AM^{30}=Adult Male # 30). Troop identities are given in double quotes (e.g. "C"="C" troop).

6.2 METHODS.

Two approaches were used to investigate the social organisation of Kanha langurs:

a/ long term monitoring of "C" troop throughout fieldwork, supplemented by ad-lib observations of adjacent troops.

b/ a census of the composition of all troops on the Kanha maidan and at Deotalao camp in April 1982.

6.2.1 LONG TERM MONITORING.

Whenever I was working in the study area "C" was observed opportunistically and any pertinent events recorded. As the all-day follows were concentrated in the second half of the month, observations from that period predominate. The composition of "C" on each follow day was known and all frequency data such as of copulations and solicitations are derived from the twelve day sample (see Chapter 3). During the first half of the month I attempted to locate and census "C" every few days although this was not always possible. Censuses were most accurately and easily carried out during single-file terrestial progressions of the troop past the observer. Censuses of resting troops were often grossly inaccurate, due to missing obscured animals, and are not used here.

All "C" langurs were individually identified although, with the exception of the hunchback IN1[54], infants could only be recognised with reference to the mother, which was assumed to be the female which suckled the infant. Infants were sexed on the basis of the absence of the groove between callosites and the presence of a nascent penis in males. The age/sex classes recognised are descibed in Table 4.A. The following features were used to differentiate between individuals:

a/natural marks such as ear notches, tail injuries and scars.

b/the terminal tail tuft (though it tended to vary with time).

c/pelage:shape of crown hair form and facial ruff, pattern of grey and in females the presence of orange chest patch.

d/depigmented blotches between thighs and on abdomen in females.

e/nipple length and differences between left and right in females.

f/body size and shape, especially face profile.

g/characteristic posture, movement and behaviour.

A notebook containing sketches, 'mugshots' with descriptions and histories was kept. All "C" langurs were provisionally identified within the first two months. All were described within four months except the four sub-adults which were distinguished by October. Distinctive langurs within other meadow groups were also described and used as markers for troop identification. (for definition of types of social grouping see 4.5).

6.2.2 LANGUR CENSUS.

During the hot weather of 1982 all langur troops found on the Kanha meadows were censused to give a sample of troop compositions and an accurate estimate of population density. An area of 7.8 sq.km., encompassing the meadows and some surrounding sal forest was divided into blocks and between 8 and 18 April each block searched thoroughly at least four times. Langurs in continuous sal forest were not censused because of the problems of langur wariness and poor visibility in such areas. The early morning 'whoop' vocalizations and the presence of chital were useful cues indicating the whereabouts of langurs. Troops were recognised by known marker individuals and their movements plotted on 1:20,000 field maps.

Three days (21-23 April 1982) were spent at the Deotalao patrol camp (see 3.1.2) to census langurs coming to drink in dry deciduous forest. Groups were censused as they progressed across the pan surrounding the lake. However, as the catchment area from which the langurs came was unknown, density and biomass could not be estimated. Censusing of troops within the hill forest would be extremely difficult due to wariness in langurs, the terrain and dense vegetation.

6.3 POPULATION STRUCTURE AND DENSITY.

6.3.1 KANHA MAIDAN.

The structure of the meadow population, given in Appendix V.A, is summarized in Tables 6.A and Fig 6.1. Eighteen groups were found, of which 14 were troops and 4 all-male bands. Of the troops all but one, a trimale, were unimale. Three other troops ("B", "L", "C") are known to have been multimale for brief periods during the study. The population consisted of 360 langurs, 304 in bisexuals and 56 in bands. The spatial distribution of these groups is shown in Figs 6.2 & 6.3 which include both census data and observations from 1981-82, with the annual range of "C" superimposed. I am confident that all troops whose entire April range was on the meadows were censused, but it is possible that peripheral troops whose range projected into the survey area from outside may have been missed.

Langur density was found to be 46.15/sq.km and group density 2.31/sq.km. The tendency for troops to be larger than bands and for a unimale troop structure to predominate is apparent in Fig 6.1. Mean troop composition was:

Troop : AM:1.1, AF:9.1, SM:1.2, SF:2.4, J:2.6, IN2:1.1, IN1:4.1

Bands : AM:8.8, SM:5.3

Biomass was calculated as :

$$\text{Biomass} = \Sigma \text{ No. of langurs in age/sex class}_i \times \text{estimated weight of age/sex class}_i$$

The weights used are given in Table 4.A. The biomass of the meadow population was 385.96 kg/km^2, consisting of 289.94 kg/km^2 for troops and 96.03 kg/km^2 for bands. Mean troop and band biomass was estimated to be 160.5 kg and 188.5 kg respectively.

The adult sex ratio for all groups was 1:2.5 (AM:AF) and for troops 1:7.9 (see Fig 6.1). No solitaries were found during the census but from April 1981 to March 1982 four solitary adult males were recorded (see Fig 6.3)

6.3.2 DEOTALAO.

The structure of the Deotalao sample is given in Table 6.B. Six troops were observed coming to drink, four unimale troops and two bands. The population consisted of 125 langurs, 91 in troops and 34 in bands. Mean group composition was:

Bisexuals : AM:1, AF:10.5, S:2.5, J:2.0, IN2:0.25, IN1:5.0.

Bands : AM:10.5, SM:6.5.

Adult sex ratio for all groups was 1:1.68 (AM:AF) and 1:10.5 for troops only. No solitaries were observed.

6.3.3 POPULATION STRUCTURE AND DENSITY : DISCUSSION.

The April 1982 census produced a detailed description of the structure and size of the Kanha meadow langur population. In this section, these results will be discussed and compared with findings from other sites. Hypotheses of intraspecific variation in social structure will be tested using data extracted from the literature. Finally, the functional significance of the unimale-multimale distinction is discussed.

It was thought possible, from opportunistic observations, that multimale troops and bands might be more frequent in the hill forest than on the meadows. Although a small sample, the Deotalao census does suggest that the hill forest and valley population structures are similar. Although density in the hills could not be estimated it is expected to be lower than in valley forest owing to the more extreme seasonality in mixed forest. If it is assumed that langur density is constant at 46.15 $/km^2$ over the entire 940 km^2 of the Park the langur population would total 43,381 animals. This is undoubtedly an over-estimate, with some areas such as the hills and Silpura supporting low langur density. The true population size probably lies between 10,000 and 20,000 animals.

The density of langurs on the Kanha meadows is in the middle of the reported range for the species. The lowest published density would appear to be 2 $/km^2$ at the Himalayan site of Junbesi and the highest at Dharwar with 135 $/km^2$ (see Table 6.C). Kanha density is similar to those reported for Polonnaruwa and Abu. Human influence on the wildlife population and habitat is currently minimal at Kanha and the langur density cannot be regarded as un-naturally elevated by deforestation, provisioning or compression. Although the meadows are anthropogenic, the slash-and-burn cultivation occurred prior to 1868 and probably in antiquity. Meadows within the sal forest have probably been characteristic of the region for some 4,000 years. Langurs spent relatively little time in the open areas (see Chapter 8) and the clearances probably reduced density; if the forest had not been broken up, a larger langur population may have been supported. If Kanha is ranked on the extent of human influence according to the scheme of Bishop *et al* (1981) the mean value for the four categories of disturbance is 1.25, with a maximum possible of 4. This compares with a value of 1 at Orcha, also moist deciduous forest, and 3.75 at Abu and Singur, both extensively altered by human activity.

Although crude, this scale does indicate that Kanha is one of the most natural habitats in which langurs have been studied. With Orcha, Kanha probably represents the closest approximation to the environment in which their recent evolution has occured.

Coe (1979) estimated that in 1976 the Park carried a terrestial herbivore biomass of some 1250 kg/km^2. Owing to high ungulate density on the meadows the biomass in the study area will be considerably higher. Langurs, or the arboreal mammalian biomass, represent > 20 % of the terrestial standing crop of mammals in Kanha. The anthropoid primate biomass at Polonnaruwa was 2,370 kg/km^2 (Eisenberg et al 1972), exceeding most wild ungulate biomass estimates for south Asia (Eisenberg & Siedensticker 1976). Similarly, in some African forests, primate biomass is comparable to terrestial folivore biomass. Struhsaker (1975) estimated that primate biomass in the Kibale forest in Uganda represented between 55 and 89 % of the ungulate biomass of the Serengeti ecosystem. With a low primate diversity in most Indian jungles, langurs commonly represent the majority of the arboreal mammalian biomass. In Kanha langurs probably accounted for >>95 %, with the only other arboreal mammal, the small palm squirrel (F.palmarum) occurring at low density. In contrast, at Polonnaruwa, out of three primate species, Presbytis entellus constituted only 31 % of mammalian arboreal biomass (Eisenberg et al 1972).

Among the colobines, Kanha langur biomass is moderate. Struhsaker & Oates (1975) estimated red colobus biomass in the Kibale forest at 1,760 kg/km^2 and black and white colobus at 64.7 kg/km^2. Eisenberg et al (1972) estimated P.entellus and P.senex biomass at Polonnaruwa at 730 and 1450 kg/km^2 respectively. In contrast P.entellus biomass at Wilpattu was only 19 kg/km^2. As shown by Clutton-Brock & Harvey (1977), colobine biomass tends to be high in comparison to that of other primates, which Struhsaker (1975) suggests may be a consequence of their digestive specializations for folivory.

Two other investigations have yielded information on the structure of the Kanha maidan population. Nagel & Lohri (1973) estimated Kanha langur density to be 20-25 /km^2 from four troops on the maidan. As no extra-troop males were included this is very probably a considerable under-estimate. Kankane (1980) in an extensive reserve wide survey in 1977, censused forty groups as tabulated below. Of thirty troops only four were multimale (with 7,3,3,2 adult males). Therefore, the population structure described in this study and by Kankane are very similar. There is a consensus that the Kanha population is predominantly unimale with a troop size of about 20, troop sex ratio of about 1:7 or 8, and extratroop males organised into bands. Kankane's (1980) study also suggests that population structure is similar across the reserve.

Variable	Kankane (1980) (reserve-wide)	this study (meadows only)
% unimale	65.0	72.0
% multimale	10.0	5.6
% bands	22.5	22.2
% solitary males	2.5	0
mean troop size (range)	17.47 (5-45)	21.7 (11-34)
mean band size (range)	8.22 (5-14)	14.0 (8-18)
troop adult sex ratio	1:6.757	1:7.9
population size sampled	599	360

As described in 4.5 a distinction has been made between unimale and multimale troops. However, Eisenberg *et al* (1972) for primate social structure in general, and Vogel (1977) for langurs, suggested that the multimale distinction is too broad and combined natural variation. Eisenberg *et al* proposed that the multimale category should be restricted to those troops having more than one functionally reproductive adult male. In contrast, many troops consist of several males of varying age with linear male dominance order and only one fully-grown adult male which monopolizes reproduction. This type, named 'age-graded male troop' by Eisenberg et al (1972) is regarded as intermediate between unimale and multimale. Vogel (1977) concluded for Hanuman langurs that most of the so-called multimale troops are in fact 'age graded'. However, the information necessary to distinguish between the two categories is not available for most sites. The difficulty has been circumvented in the following discussion by expressing the troop organisation in terms of the proportion of unimale troops.

A great range of langur population structures have been described and are listed in Table 6.C, grouped by habitat.The Kanha statistics refer only to the meadow population; the small Deotalao census is not included owing to the lack of a density estimate. The syntheses of Vogel (1977) and Oppenheimer (1977) used sites irrespective of considerable variation in sample size, study completeness and duration. Therefore, before the table was drawn up a subset of nine roughly equivalent sites were selected in which the study was long term (> 9 months), with large sample sizes and a large amount of diverse published information. In the following analysis of intraspecific variation this subset of 'detailed' sites is regarded as yielding more reliable information and hence correlations are considered at the two levels of 'detailed' sites only and all sites. The relation of the Kanha population structure to the published range of variation will be considered and then various hypotheses of intraspecific variation tested.

Kanha troop size at 21.7 is within the lower range of variation with a mean for all sites of 29. The smallest troop recorded appears to be five (Oppenheimer 1977). Band size, as elsewhere, is consistently smaller on average than troop size (Mohnot et al 1981).

Intraspecific variation in range size is discussed in 8.4. The percentage of unimale troops was calculated as the percentage of troops with only one adult male. Kanha has one of the highest proportions of unimale troops of any langur population yet studied. The troop adult sex ratio is expressed as the number of adult females per adult male. As langur males mature to adult status at about twice the age of females the sex ratio would be expected to be biased in favour of females (Marsh 1978). The Kanha adult troop sex ratio is one of the most disparate yet reported for langurs. If the entire meadow population is considered there are still 2.5 times as many adult females as males. If males do not move from the study area this disparity is presumably the result of differential mortality. The percentage of adult extra-troop males is expressed as the percentage of males living outside troops out of the total complement of this age/sex class in the population. As expected from the prevalence of unimale troops, the majority of males live outside reproductive groups. The level of such band males is high in Kanha in the species range. The band:troop ratio, calculated as the number of troops observed per band, is of medium value in Kanha. This measure is probably, like % of extratroop males, sensitive to differences in the observers ability to find the more fluid, wide ranging bands as opposed to the more stable, philopatric troops.

Therefore the Kanha meadow population, in comparison to conspecifics elsewhere, has moderate density, troop and band size but has a very high preponderance of unimale troops. The troop sex ratio is very disparate and a large proportion of the adult males live outside troops. Sugiyama (1965a,b), Yoshiba (1968), Hrdy (1977b), Vogel (1977) and Boggess (1980) have suggested a series of correlations that might be expected amongst these variables. Below some of the hypotheses will be evaluated with respect to the data in Table 6.C.

A. **Larger troop size is found in open vegetation type.** Ripley (1970) and Vogel (1977) suggested that the mean langur troop size is larger in relatively open habitats such as open scrub, deforested areas and high altitude landscapes. This was interpreted as a consequence of increased risk of predation in open environments and the increased protection afforded by living in large groups (Bertram 1978) when terrestrial. A similar association has been suggested for savanna versus forest primates from inter-specific comparisons (Crook & Gartlan 1966) but size and dispersion of food clumps (Clutton-Brock & Harvey 1977) and degree of seasonality and aridity may also be important (Crook 1970).

Inspection of Table 6.C does suggest that the largest troops have been recorded from relatively open peninsular habitats, but it is inconsistent, with some open sites bearing small troops and forests bearing large troops. Before any relationships can be confidently asserted more accurate quantification of 'open' is required, perhaps in terms of tree basal area (see Chapter 5).

B. **Higher population density is found in open vegetation types.** At Dharwar, Sugiyama (1964) found that the langur population density in dry deciduous forest was about five times higher than that in more open vegetation (cultivation,meadow,scrub). It was suggested that the disparity was a consequence of the forest having a higher 'environmental value' with the open habitat full of 'space' which could not be exploited by langurs. Vogel (1977) was unable to find a correlation between density and vegetation type across Asian habitats. Bishop (1979) noted generally low density in the high Himalaya and suggested that it was probably a consquence of seasonally sparse and patchy food resources. The data shown in Table 6.C suggests that low Himalayan density is the only consistent feature; there is considerable variation amongst the peninsular populations. For example the three moist deciduous forest sites have densities of 6.2, 46.15 and $80/km^2$, spanning most of the species range. Broad vegetation classification is unlikely to be closely related to density as such terms as 'forest' lump many very different habitats (Clutton-Brock 1974a).

C. **The proportion of extra-troop males is positively related to the proportion of unimale troops present.** If troops are predominantly organised as unimale, the excluded adult males could either die, emigrate, form bands or become solitaries. If the latter two possibilities occur, it would expected that the greater the level of unimale structure, the higher the proportion of males that would be found living outside troops. Deviations from a proportional relationship could result from death or emigration of excluded males or from sampling errors. As bands are more mobile than troops, a large area, perhaps larger than generally covered in langur studies, would have to be sampled in order to include the appropriate extra-troop males. Sugiyama et al (1965) found evidence that bands occupied habitat of 'low ecological value', not visited by troops. Boggess (1979) noted that those sites with low levels of extra-troop males (< 40%) were predominantly unimale, but sites with high levels of extra-troop males (> 40%) were variable in troop pattern.

The data from Table 6.C for the percentage (hereafter '%') of extra-troop adult males and % of unimale troops is plotted in Fig 6.4. The nine 'detailed' sites, with the exception of Rajaji, show a strong relationship in support of the hypothesis. Considering the entire data set Bhimtal and Sariska also deviate considerably. The review does suggest, for the more reliable sites, a curvi-linear relationship between the proportion of males living apart from females and the prevalence of unimale stucture.

D. **Imbalance of troop adult sex ratio is positively related to the proportion of extra-troop males and the proportion of unimale troops.** Boggess (1979) suggested that low levels of extra-troop males are associated with a less disparate adult troop sex ratio. The relationship is shown in Fig 6.5 and for the 'detailed' sites there is a tendency for sites with <50 % extra-troop males to have a less imbalanced sex ratio than those with >50 % excluded males. There is a significant relationship (r_s=0.759,P<0.05,n=8).

Vogel (1977) claimed that the most disparate troop adult sex ratios were found at sites where unimale structure predominated. This relation would seem to be a logical demographic consequence given that, apart from very rare occasions, females exist only in troops. The relationship is plotted in Fig 6.6 and a linear association is suggested with all sites and the 'detailed' sub-set giving significant correlation coefficients (r_s=0.924,P<0.01,n=8; r_s=0.687,P<0.01,n=14).

Therefore, the predicted trends between sex ratio and the proportion of unimales and extra-troop males are found but only the former pair shows any evidence of a significant linear relationship. The low significance of relationships may be the result of ill-understood population processes and insufficient sample sizes.

E. Band size is positively related to the proportion of unimale troops. Vogel (1977) suggested that the largest bands occurred at sites where troops are predominantly unimale. If all extra-troop males were organised into bands (with a few or no solitaries) then with increased unimale character larger bands and/or a larger number of bands would be expected. In Fig 6.7 and 6.8 band size and band:troop ratio are plotted against the percentage of unimale troops. Band size is known for relatively few sites but both data sets suggest significant linear relationships (r_s=0.814,P<0.01,n=10; r_s=0.958,P<0.001,n=7). In contrast the band:troop ratio is not significantly correlated with the proportion of unimale troops for either data set (r_s=0.282,P>0.05,n=6; r_s=0.446,P>0.05,n=12) (although a highly significant result arises if Kanha and Jodhpur are excluded). There appears to be a tendency for band size but not the number of bands to increase with an increased level of unimale structure.

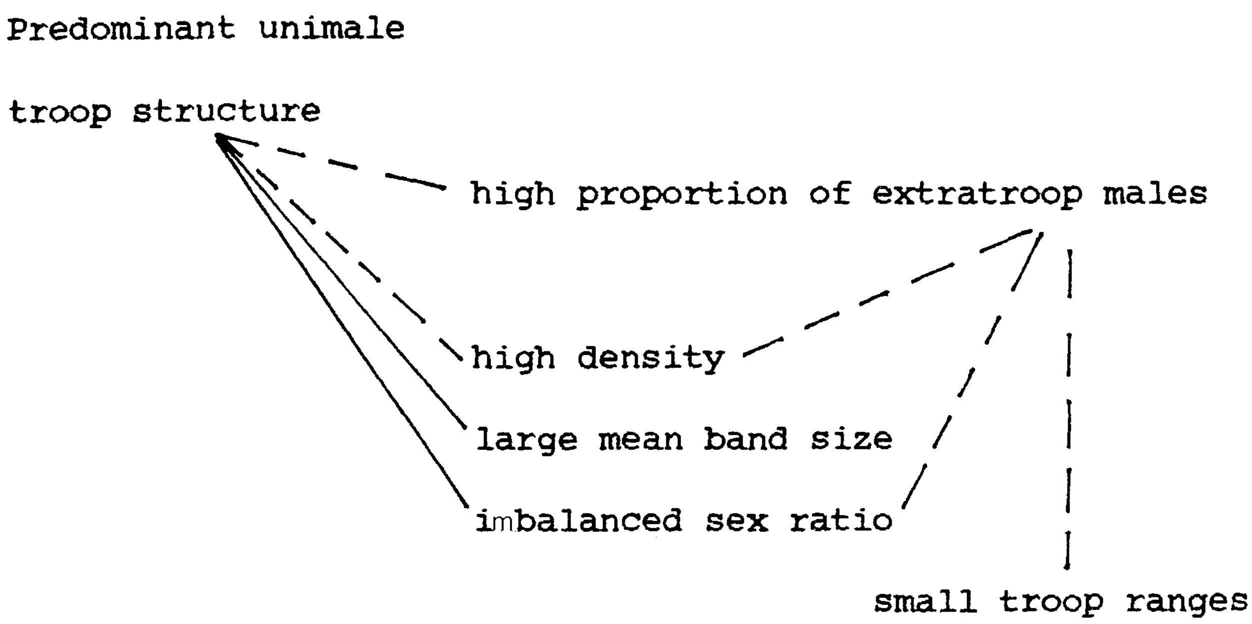
F. The proportion of unimale troops is positively related to population density. Yoshiba (1968) suggested that at high densities langurs are predominantly organised into unimale troops. Hrdy (1977) noted "a striking (but not perfect) correlation between low population density and the existence of multimale troops". The data for all sites is plotted in Fig 6.9 and the 'detailed' subset shows a possible, but insignificant linear relationship (r_s=0.336,P>0.05,n=9). It is clear for the 'detailed' data that the higher density sites (> 20/km^2) tend to have a predominantly unimale structure. Sites of low density (< 20/km^2) consistently have a predominantly multimale (or age-graded) organisation. This hypothesis is supported by the observation at Dharwar, that with a fall in langur density the proportion of multimale troops increased (Hrdy 1979).

G. **The proportion of extra-troop males is positively related to population density.** Yoshiba (1968) and Hrdy (1977b) suggested that higher proportions of males lived outside troops at higher population densities. However, Vogel (1977) was unable to confirm the hypothesis from a large selection of sites. Boggess (1980) noted that density is not absolutely correlated with percentage of extra-troop males but that sites with few such males tended to also have low density. The relationship is plotted in Fig 6.10 and shows an insignificant tendency (r_s=0.559,P>0.05,n=9) among the 'detailed' subset for low densities to be associated with low levels of extra-troop males.

H. **Imbalance of troop adult sex ratio is positively related to population density.** Vogel (1977) could not confirm his hypothesis that the most unbalanced troop sex ratios occurred in high density areas. The relationship is plotted in Fig 6.11. For the detailed sites there is a tendency for such an association but it is insignificant (r_s=0.524,P >0.05,n=7).

I. **The proportion of extra-troop males is inversely related to troop range size.** The curvi-linear inverse relationship between range size and density is described in 8.4. Boggess (1980) noted that above a range size of some 1.9 km^2 a low proportion (< 40%) of extra-troop males occurred in the population whilst below 1.9 km^2 high proportions (>40 %) of such males were found. The data set, shown in Fig 6.12, suggests that among the 'detailed' sites a curvi-linear, inverse relationship exists, confirming Bogess'(1980) suggestion.

The above testing of population structure hypotheses only yields two significant linear correlations. Some relationships are curvi-linear but others show considerable unpatterned scatter. This may reflect the absence of a relationship or inadequate sampling of the langur populations, especially if there is any spatial segregation of bands and troops. The figures did reveal a number of gross tendencies of association among the nine 'detailed' sites as summarized below :



—— significant linear correlation P <0.05

---- observed tendency for association and curvi-linear relationships.

Despite many thousands of hours of langur watching at some seventeen sites, the determinants of the great variation in langur social organisation are not understood. What is cause and what is effect is not clear. In particular, the functional significance of the unimale-multimale distinction has defied convincing explanation. Yoshiba (1968) suggested that multimale troops occurred at sites with high risk from predators, presuming that adult males were valuable in deterring attacks. Intra-specific variation in langurs does not support this hypothesis: Orcha and Kanha, the two sites with the largest complement of predators are at opposite extremes of the unimale - multimale spectrum. Indeed, increased numbers of troop adult males would seem unlikely to decrease predator risk in arboreal primates (Aldrich-Blake 1970).

Sugiyama (1965b) and Oppenheimer (1977) suggested that multimale troops occurred in more 'favourable environments' than unimale troops. The unimale condition was originally proposed, from inter-specific comparisons, to be an adaptation to seasonally arid environments in grasslands (Crook & Gartlan 1966,Crook 1970). It was argued that in food shortages reduced numbers of males in a troop would be advantageous by minimising intra-group competition whilst the single male could potentially fertilize all the females (Coelho et al 1977, Gartlan & Brain 1968). However, Clutton-Brock & Harvey (1976,1977) noted that the food shortage or 'group economic advantage hypothesis' is difficult to state in terms of individual advantage and appears to require group selection, which is unlikely to be acting in leaf monkeys (Maynard-Smith 1976). Since the reviews of Crook & Gartlan (1966) it has been shown that many forest dwelling colobines and cercopithecines also have a unimale structure (Struhsaker 1969). However, Aldrich-Blake (1970) and Crook (1970) argued that this revelation is not inconsistent with the original hypothesis, as forests are not uniform habitats with a super-abundance of food. Indeed, food availability in forests is likely to be very heterogeneous in time and space. Clutton-Brock & Harvey (1977) note that it is difficult to explain variation in unimale-multimale structure by any unitary hypothesis. Similarly, functional reasons for variation in the organisation of langur troops are unclear. The unimale-multimale distinction will be returned to when considering social change (6.8).

Within the colobine sub-family twelve of the fifteen species listed in Hrdy (1977b) occur both as unimale and multimale troops with probably a tendency for the former to predominate. The three exceptions are Presbytis potenziani, which most idiosyncratically, form monogamous pairs, Colobus badius which generally form large multimale groups (though see Marsh 1980) and Nasalis larvatus which form small multimale groups. Of the south Asian colobines P.geei, P.cristata , P.johnii and P.senex are predominantly unimale with bands recorded. In the Cameroons, Struhsaker (1969) found that cercopithecine forest species tend to form unimale troops with solitaries whilst open country species tended to form multimales. Struhsaker suggested that the absence of solitaries in open country species is related to higher predation risk in grassland as opposed to forest.

The general colobine and forest-dwelling cercopithecine tendency appears to be the formation of unimale troops of between 10 and 30 animals, with extra-troop males existing mostly as bands in the former and solitaries in the latter. Apart from the three exceptional colobine species, Hanuman langur population structure spans the entire range found within the subfamily. A preponderance of unimale Hanuman troops is associated with high levels of extra-troop males, disparate adult troop sex ratios, large band size and tentatively with high density. Similarly high levels of extra-troop males are associated with small range size. Convincing functional explanations for the extensive variation in langur social organisation have yet to be demonstrated.

6.4 REPRODUCTION AND MORTALITY.

Known losses and gains to "C" troop by births, deaths, transfers and disappearances are summarized in Appendix V.B and Fig 6.13 shows monthly variation in troop size and the frequency of membership changes. The relationships between "C" troop langurs are given in Appendix V.C and the histories of individual females and their offspring are shown in Appendix V.D.

6.4.1 REPRODUCTION : RESULTS.

Soliciting, in which a female presents her rump towards a male whilst rapidy shaking her head (Dolhinow 1978), is indicative of estrus or pseudoestrus and was observed throughout the year. Its temporal distribution (Fig 6.15) is bimodal, peaking in May and August. Matings were confined from April until August and October, with a median on 14 July. The temporal distributions of matings and solicitations were similar, apart from the restriction of copulation to the monsoon and late hot weather. Sexual activity was highest from May to August. Of 295 solicitations observed all but 6 were given to the "C" adult male. The exceptions were five given to AM^{Q} and one to AM^{L}. Of 35 copulations observed, 32 were with the troop male. The exceptions were AM^{24} with AF^{29}, AM^{Q} with AF^{11} and AM^{L} with AF^{31} but this adultery was, assuming a 200 day gestation (Hrdy 1977b), unlikely to have resulted in conception. All copulations were solicited by the female and harassment of mating pairs by adult and sub-adult females was frequenty observed (Hrdy 1977b). Births were observed from December to May, with January the most prolific month. The median of the birth distribution is 25 February in Fig 6.14. No neonates were recorded in any Kanha troop outside the months of December to May which suggests a pronounced birth season. One exception was F^{25} which was estimated to have been born in August 1980.

The differences between the above medians gives a copulation-birth interval of 225 days and a solicitation-birth interval of 180 days. Parturition was not observed but, as four of the nineteen births occurred between the observers presence at dusk and the following dawn, nocturnal births are likely. I was never able to predict imminent birth or even pregnancy from female body shape. The birth sex ratio was 1:1 (9 male,9 female,1 of unknown sex).

Individual histories (Appendix V.D) are incomplete as "C" was only intensively observed for 12 days a month. However, the information for eight females (11,28,29,36,38,39,42,45) is sufficient to estimate the gestation period. The interval was calculated as the time between the last observed copulation before birth (or for AF42 the peak in solicitations) and the estimated date of parturition. Mean gestation period was estimated at 171.4 ± 31.0 days (139-205 days range). If gestation is of this order of magnitude it is evident that the majority of females show post-conception estrus with, for example, AF^{29} solicited in the same month as it gave birth (see Appendix V.D). No quantitative differences were noted between soliciting prior to conception and during pregnancy.

This study was of insufficient duration to produce much detailed information on intervals between births. However, the birth interval between the bearing of F^{35} and F^{76} by AF^{5} was about two years. The interval between the birth of F^{25} and M^{78} to AF^{22} was estimated to be 29 months. The first infant born to each of these females during the study is known to have survived to weaning. Six infants disappeared from "C" and mothers were known in three cases and probably known in two. The identity of the mother of one infanticide victim was unknown. All five females gave birth again during the study as tabulated below:

Female	First Infant Birth date	First Infant Missing date	Second Infant Birth date	Birth Interval	Death-Birth Lag
AF28*	2/4/1981	18/4/1981	15/1/1982	9.6 months	272 days
AF29*	late/2/81	21/4/1981	19/3/1982	11	332
AF42+	"	01/9/1981	12/4/1982	14	223
AF36+	"	30/7/1981	03/3/1982	12	216
AF39+	19/1/1982	21/5/1982	?/1/1983	12	240
Mean ± s.d.				11.7±1.61	256.6±47.4

[*:infanticide, +:infant disappearance in unknown circumstances.]

Calculations are based on the earliest possible date for each event. Birth interval is the interval between subsequent births for the same female; death-birth lag is the interval between infant disappearance and subsequent birth for the same female.

Therefore the five females show, albeit from crude information, that mean birth intervals for infant-deprived females was about one year and that the lag between infant loss and next birth was some eight months

6.4.2 REPRODUCTION : DISCUSSION.

Kanha langurs showed considerable reproductive seasonality. Birth in the cold and hot weather, but rarely in the monsoon, appears to be usual for most langur populations as shown in Fig 6.17. Although at some sites births were recorded throughout the year, birth peaks generally occurred within the period of December to June. Monsoon birth peaks only occurred at Abu and Jaipur and then in addition to hot weather peaks. The general consistency in birth season presumably reflects entrainment by the environment, perhaps to give high food availabilty at gestation, lactation or weaning onset. It is difficult to arrive at convincing functional explanations for the timing of reproduction, in the absence of detailed information on forage quality and animal requirements. The early gestation and onset of infant solid food consumption occurred during the relatively high protein, low energy monsoon diet (see Chapter 9) whilst most of the gestation and early lactation spanned the relatively high protein, low energy winter and low protein, high energy hot weather. Pronounced birth seasonality is not confined to the Himalayan populations (see Fig 6.17) as suggested by Bishop (1979) and is at variance with Hrdy's (1977b) conclusion that strictly seasonal births do not occur.

Social factors may also be important. Sugiyama (1965b) and Hrdy (1977b) suggest that, like some other primate species, langur females within a troop tend to synchronize their reproductive cycles so that within troop birth date variation is less than between troops. The loss of an infant, as discussed below and in 6.6-6.8 generally results in an early return to sexual receptivity. Hrdy (1977b) and Sugiyama (1965a) noted that the entrance of alien males into a troop may trigger continuous estrus behaviour, irrespective of normal menstrual cycling. The temporal distribution of solicits and copulations in "C" troop females matches the distribution of births some six months later. It is possible that the May peak in solicits, without a corresponding birth peak may have been related to the invasion by "Q" (see 6.7) .

The estimated copulation-birth intervals, calculated from the frequency distributions and from individual female histories are close to the 200 ± 10 days gestation period calculated for captive and free-ranging animals (Hrdy 1977b). However, the interpretation of soliciting behaviour is complicated by pseudoestrus. As noted in 4.7 external manifestation of the monthly menstruation cycle is rare and hence confirmation of reproductive state, independent of behaviour, is hard to achieve. Estrus is used here to refer to behaviour and not physiology.

Pseudoestrus is inferred when backtracking from a birth indicates that the female was pregnant when showing estrus behaviour (Hrdy 1977b). The individual histories of "C" females strongly suggests that males were solicited during pregnancy, even in the month when they gave birth. It is also possible that females solicited, when not pregnant, out of phase with their reproductive state. Post-conception estrus has been described for a variety of primates and for langurs at Abu (Hrdy 1977b), Dharwar (Sugiyama 1965a) and Jodhpur (Mohnot 1971a). Interpretation of this behaviour depends on whether males can discriminate between true and pseudo-estrus. I could detect no distinction in the form of the solicit between pre- and post-conception estrus but any differences may have been missed as the latter category could only be identified, in retrospect, once parturition had occurred. It is therefore possible that human observers combine together a variety of behaviours under the term solicit. Hrdy (1977b) noted that head shaking by pseudoestrus females is usually less pronounced than in those in physiological estrus. If males can discriminate, pseudoestrus may be a form of appeasement behaviour. If they cannot the females may be deceiving males for reasons discussed in 6.7.

Single births appeared to be the rule at Kanha with twins never observed, although they have been recorded elsewhere (Roonwal & Mohnot 1977). The two birth intervals, in which the first offspring survived to weaning, at 24 and 29 months are similar to Jay's (1965) estimate of 20-24 months and Hrdy's (1977b) of 20-30 months. The interval is the sum of gestation, lactation and a lag, although Hrdy (1977b) records that females have occasionally conceived whilst lactating. The comparison of birth intervals with and without infant loss, 11.7 months versus 26.5 months respectively, suggests considerable acceleration of subsequent birth induced by infant removal. If the gestation period is 200 days, the data suggest that females conceive, on average two months after infant loss, with a minimum lag of 16 days. Ripley (in Roonwal & Mohnot 1977) noted a female coming into estrus within fourteen days of the death of its infant. Mohnot (1971a) noted that all three infant-deprived females came into estrus an average 6.5 days after infant death with a minimum delay of 28 hours and a maximum of eleven days. However, the average interval between between infant death and the next live birth from the same females was 17 months, suggesting a ten month delay in conception (Mohnot 1971a). Hrdy (1977b) suggested that this lag was imposed by the harsh desert conditions at Jodhpur. Hrdy (1977b) reviewed Dharwar and Jodhpur birth intervals and found that on average there was a lag between infant death and the mothers subsequent estrus of eight days and between infant death and subsequent birth of 10.5 months (7.2 months if Jodhpur is excluded). Some of this variation may be result of seasonality in breeding season. In environments where the timing of birth greatly affects the success of the offspring or the cost to the mother it may be in the females interest, despite the delay, to wait to breed at the optimal time. Conception may therefore be delayed until the next breeding season, lengthening birth intervals.

All but two "C" females which showed estrous behaviour subsequently gave birth. The exceptions were SF^{52} which disappeared between July 1982 and April 1983 and AF^{31} which despite extensive solicitations and seven observed copulations in the 1981 monsoon, failed to bear young (it is however possible that birth and death of an infant occured during the observers absence). The female, on the evidence of pendulous nipples, had borne young previously, but was perhaps now defective and unable to conceive.

Of the numerous solicitation bouts observed the vast majority were directed towards the single adult male of "C" (AM^{23} and then AM^{30}). Similarily only 8.6 % of copulations were adulterous, the majority of which was with "Q" males in the hot weather of 1981. There was only one solicition or copulation to a non "C" or "Q" male and that was AF^{31} with AM^{L}. This may have been related to the difficulty AF^{31} was apparently having in conceiving. In such a situation the best strategy may be to be promiscuous in case the consort is infertile or incompatable. Assuming a gestation period of 200 days none of the three adulterous copulations could have resulted in conception. Although I was only present with "C" for 40 % of the daylight hours from April 1981 to March 1982, the very low level of extra-troop copulations does suggest that the "C" adult male did father most, if not all, of the troops' births. Langur adultery will be returned to in 6.7. in considering "C"-"Q" relations.

6.4.3 MORTALITY : RESULTS.

Death is very rarely observed in primate populations and consequently information on the causes and rates of mortality is sparse. Disappearance of an animal from a troop during the observer's absence is difficult to interpret, as the animal may have died or emigrated. However, the disappearance of infants in the continuing presence of the mother does suggest infant death. Kidnapping (Mohnot 1980) was not observed in Kanha. The small amount of information available from "C" is shown in Fig 6.13 & 6.16 and detailed in Appendix V.B. Disappearances and mortality observed in "C" and other troops is described below.

"C" troop:

a/ Infanticide: In April 1981 three infant-ones were killed by adult males of the "Q" all-male band. This is further described in 6.7.

b/ Infant disappearances: Apart from the above infanticide three infants went missing from "C", $IN2^{46,47}$ and $IN1^{58}$. The estimated infant mortality for the study duration was 6 out of 19 born or 31.6 %, of which half were due to infanticide.

c/ Adult & sub-adult disappearances:On May 5 1981 AM^{23} disappeared from "C" and AM^{30} immigrated from band "Q". AM^{23} was never seen again and was regarded as missing, presumed dead or emigrated. The circumstances of this takeover are further descibed in 6.4.4. Between 20/6/1982 and 9/4/1983 SF^{52} went missing from "C", presumed dead or emigrated.

Other troops:

a/ Non-expelled stillbirth:On 27 May 1980 a "B" troop adult female was observed with the clenched fist and forearm of an infant protruding from her vulva. In two hours of intermittent watching no movements were seen in the infant's hand, despite being sat upon and becoming an attraction for flies. Although this indicated a still-birth, there were no signs of expulsion of the infant. The mother touched the limb repeatedly and lightly pulled; other females also examined the arm. The adult female moved some 250m away from the rest of the troop and was never seen again, presumed dead.

b/ Electric shock:An 8.0 kg adult female, probably of "CH" troop was killed by touching mains power lines leading to Kanha village on 2 April 1982.

c/ Fire: On 28 April 1980 a langur was killed on being trapped in an isolated tree during a grass fire on Rondha maidan (Ilias pers.comm.)

d/ Predators: Dr P.C. Kotwal (pers.comm.) in an analysis of 237 tiger faeces, obtained from throughout the Reserve, found langur hair in 13.5%. On 2 September 1980 an Indian python (*Python molurus*) constricted and swallowed a troop adult male in dry deciduous forest at the ghat between Kanha and Kisli villages (Chandrimani pers.comm.). On 12 June 1980 I observed a panther (*P.pardus*) unsuccessfully hunt a langur troop in sal canopy in the Kuloo chattan study area (at 23/22 grid cell) at 08.00 hours. All langurs remained arboreal. On 22 April 1981 during a "C"-"M" encounter an infant-two of "M" ran towards "C" into a stream bed where a jackal (C. aureus) attacked it and carried it off. The jackal ran some 250m, with AM^M chasing for about 100m, before stopping to eat the langur. Jackals and panthers are probably the major predators of langurs in Kanha.

e/ Falls: In over 2000 hours of observation only two falls of greater than fifteen metres were witnessed. $AF^{22}IN2^{25}$ was seen to fall 15-20 m during an inter-troop encounter in 1980. AF^{22} landed quadrupedally with the infant remaining on its chest, both escaping injury. On 18 April 1981 $IN1^{17}$ was seen to fall some 20 m during a "Q" infanticide attack (see 6.7). Although perhaps contributing to its injuries, it was thought that the fatal damage was inflicted by the band adult males. Falls are therefore probably not an important cause of mortality in sal forest but may be important in the hill forest which has a more fragmented canopy.

6.4.4 MORTALITY : DISCUSSION.

There is very little information available on primate mortality, particulary of rates. Most of the data are opportunistic and anecdotal.

Infanticide has been reported for Hanuman langurs at three other sites in a similar context to that observed in Kanha (see 6.5). At Mount Abu, Hrdy (1977b) suggested that infanticide by invading males was the single greatest cause of mortality. This is considered in more detail in 6.5-8. Electrocution from domestic power lines was also a serious hazard at Abu and is probably a major cause of death among urban primates. Mohnot (1971a) observed mass langur mortality in Rajasthan, perhaps as a result of the animals drinking water poisoned with algal toxins (Oppenheimer 1977). Mass langur mortality has also been observed in outbreaks of the Kaysanur Forest Disease in south India. Langurs may be involved in the maintenance of this tick-borne arbovirus, which also causes substantial human mortality (Boshell 1969).

Although rarely observed, tigers, panthers, lions, jackals, pythons (P.molurus) and crocodiles (C.palustris) in forest areas and pariah dogs (C.familiaris) around villages are probably important causes of mortality. Working in Kanha, Schaller (1967) found that 6 % of the tiger faeces and 27 % of the panther faeces containing langur hairs. During the sighting of the panther hunting arboreally all the monkeys remained above about 10 m in the trees. This is in contrast to the frequently reported behaviour of langurs dropping to the ground during panther attacks, where paradoxically they would seem easier prey (Brander 1939, Pythian-Adams 1940, Roonwal & Mohnot 1977). It is also likely that, before the extensive Hinduization of the Highland's tribals, within the last few centuries, hunting of langurs by man was more frequent than at present. It is possible that crested serpent eagles (Spilornis cheela) and crested hawk eagles (Spitcaetus cirrhatus) could carry off infant langurs. Anti-predator vocalizations were frequently heard on the meadows (at least several times a day) and some semantics appeared to be involved (Seyfarth et al 1980) with characteristic alarm calls given to large low flying birds such as raptors, vultures and hornbills. I could discriminate these calls from those given on sighting mammalian predators. Mortality information among other colobines is similarily largely anecdotal, without quantification of rates. Similar factors such as predators, disease and falls are likely to be involved.

The combination of birth, death, transfer and disappearance resulted in "C" doubling in size in the two years of the study from 14 to 29 animals (Fig 6.13). The growth of "C" may not have been typical of other, longer established, troops as "C" was probably founded six months before the onset of intensive recording. There is evidence of seasonality with troop size increasing during the birth season and subsequently declining slightly as a result of neonatal mortality. Therefore, in conclusion, monitoring of "C" troop provided evidence of pronounced seasonality, of pseudo-estrous behaviour and of shortened birth intervals for infant-deprived females. Observations suggested that death due to factors such as infanticide, fire and predation were involved, but their relative importance could not be gauged owing to a small sample size.

6.5 SOCIAL CHANGE AND INFANTICIDE: EVIDENCE FROM THE LITERATURE.

In 6.4.3 it was noted that infanticide was an important cause of mortality in "C" troop. The remainder of this chapter is concerned with social change and infanticide. This topic is concentrated upon because it has proved one of the most intersting and controversial aspects of langur biology.

Firstly, in this section, patterns of langur social change and infant killing, described in the literature, are reviewed. Secondly, in 6.6, the hypotheses proposed to account for infanticide are described. Thirdly, in 6.7 the observations of infanticide in Kanha will be presented and discussed with respect to these hypotheses. Fourthly and finally, in 6.8, infant killing in other mammal species is compared with the phenomena in langurs and the reasons for variability in the incidence of this behaviour in langurs is discussed. In Appendix III a draft of a paper on langur infanticide is included; it may be useful as an extended summary of the essentials of this chapter. In Appendix IV the field notes for the period of "C" troop - "Q" band encounters are summarized for reference.

Hanuman langurs are characterised by fluidity in male membership of troops; females consistently remain in natal troops, forming a stable core. However, populations show considerable variation in patterns of male social change; three main categories have been observed in the wild:

a) gradual introductions and exclusions of adult males e.g. Junbesi (Boggess 1980).

b) rapid adult male replacement or 'takeover' e.g. Dharwar (Sugiyama 1965a).

c) band-troop associations during the mating season with low levels of intermale aggression e.g. Rajaji (Laws & Vonder Haar Laws 1984).

Some aspects of these patterns pertinent to the Kanha observations are considered below. The main types of social change are classified in a scheme, illustrated diagrammatically in Table 6.18. Population characteristics for each site are given in Table 6.C and takeover characteristics in Table 6.D.

6.5.1 GRADUAL MALE REPLACEMENT.

Boggess (1980), working at Junbesi in the high Nepalese Himalaya, found that as a result of intermale aggression, gradual but complete adult male replacement occurred, with a staggered pattern of introductions and exclusions. Multimale troops tended to become unimale during the mating season. Extra-troop males occurred as solitaries and not as bands. Boggess (1979) suggested that a similar pattern also occurred at the Himalayan sites of Simla, Bhimtal and Melemchi, the peninsular sites of Orcha, Kaukori and Gir and the Singalese site of Polonnaruwa. McCann (1933) also noted that troops tended to be multimale outside the mating season but with the onset of breeding a male expelled all other males, which then formed bands.

6.5.2 RAPID MALE REPLACEMENT OR TAKEOVER.

In contrast to the above gradual pattern of male replacement Sugiyama (1965a,b), Mohnot (1971a) and Hrdy (1977b) have reported rapid change or takeover, often associated with infant disappearance and occasionally with observed infanticide. In the general case, as suggested by Hrdy (1977b), a troop-band encounter results in the sudden replacement of the troop resident by a band male. In the following text the evidence for rapid social change at Dharwar, Jodhpur and Abu will be considered in some detail as its description is necessary before discussing the social change observed in Kanha.

Dharwar:Karnataka.

Between 1961 and 1963 Sugiyama (1964,1965a,b,1966,1967) reported ten major social changes in troops observed near Dharwar. Of these, three have here been classed as 'takeover', two as 'merging takeover' (which were artificially induced), two as 'divisive takeover' and three as 'reduction of multimale' (see Fig 6.18).

The first langur takeover to be reported in detail was that of troop "30" by Sugiyama (1965a). In May 1962 a seven member band attacked a large unimale troop, severely injuring the resident. Following further attacks in the subsequent ten days, the resident and six juvenile males left the troop. During the following week six males of the band also left, leaving one of their number behind as resident. In the following two months all five infants and a juvenile female disappeared. The injuring of one infant by the new male was observed and it subsequently disappeared, presumed died of wounds. Of the remaining five infants all disappeared, one observed bearing wounds. The new resident frequently attacked adult females with and without infants.

In the case of troop "1", a two-member band took over the trimale troop and four or five infants disappeared in the following month.

In the case of troop "7" three adult male ousted the single resident creating a multimale but after a month two males disappeared. The new resident attacked all six infants but none disappeared (Sugiyama 1965a,b,1967).

Sugiyama (1966) experimentally removed the adult male of troop "2", precipitating events classified here as a 'merging takeover'. A week after the removal of the male the adjacent troop "4" attacked "2"; all four infants disappeared within four days. Actual wounding was not observed but injuries were noted on two infants before they went missing. The "4" male was seen to chase and grab at infants being carried by females. Subsequently, this male tried to merge "2" and "4" but failed owing to the female core of each troop continuing to range independently. Three months after the removal, the "4" male rarely visited the male-less "2". However, the resident of another adjacent troop, "3", initiated another 'part time takeover' and successfully merged the two troops (Boggess 1979).

An adult male, either a solitary or from a band, attacked the unimale troop "40" resulting in severe injuries to both adult males and precipitated events categorized here as a 'divisive takeover'. The invader 'decamped' with most of the "40" females including two infants and formed a new troop which ranged nearby the reduced "40" (Sugiyama 1964,1967). A similar result occured when a large band of 59 males attacked troop "5" and three or four other adjacent troops. Females from each bisexual joined the males and formed a new multimale. Subsequently the troop was reduced, by male emigration, to a unimale structure (Sugiyama 1967).

Therefore a considerable variety of social change was encountered at Dharwar. One infant was observed to be injured and later disappeared. Of the 12-13 other missing infants, three were seen to bear wounds. No infants were seen to be wounded in any other circumstances. Sugiyama (1966) estimated tenure length of adult males in troops as 3-5 years whilst Sugiyama (1967) estimated 27 months. Sugiyama (1965a,b,1966,1967) showed that after takeovers there was a substantial increase in sexual activity in the form of solicitations and matings with the new resident. After the takeovers of "2" and "30" eight of the ten infant-deprived females gave birth within eight months. Hrdy (1977b) calculated a mean lag of nine days between infant loss and first subsequent estrus for "2" and "30" females. The average interval between births, in which the first infant failed to survive to weaning, was 16 months whereas the birth interval with survival to weaning was some 20-24 months (Boggess 1979). Although much of the sexual activity coincided with the mating season in this locality, the apparently aseasonal sexual behaviour after troop "7" takeover does suggest that sexual activity is linked to takeover (Sugiyama 1967).

As Boggess (1979) noted there is virtually no paternity data for the infants which disappeared, presumed dead. It would seem most likely, however, that the father was not a member of a band, but the resident prior to takeover. The paternity of infants born after male change is also uncertain in many cases. Backtracking from births suggests that on some occasions the previous or new resident or band males could have been responsible. Boggess (1979) judges that of troop "2" and "30" the invading male is likely to have been the father of five out of eight post-takeover births but paternity is in doubt for the remainder. Infants born less than 200 days after the takeover were never seen to be attacked by the new male, although the latter is very unlikely to have been the father (Yoshiba 1968).

Jodhpur:Rajasthan.

Mohnot (1971a) and later Makwana (1979) and Makwana & Advani (1981) have conducted a long term study of langurs living in the vicinity of Jodhpur. Reductions of multimale to unimale were observed by Mohnot (cited in Oppenheimer 1977), achieved by emigration of 25 males and by Makwana & Advani (1981) for troop "Vidyasal-A". However, other unobserved changes must have been involved in the latter change as an additional 21 animals disappeared. Adult female transfer was noted twice by Makwana & Advani (1981) with on one occasion a female moving from a male-less troop ("SH") into a neighbouring unimale.

Seven 'takeovers', and one each of 'merging' and 'divisive takeover' have been reported from Jodhpur. The first unequivocal observations of infanticide in langurs were reported for troop "B26" by Mohnot (1971a). This troop was reduced from 82 langurs to seven adult females and four infants, within a week, perhaps by algal toxins in drinking water (Oppenheimer 1977). Nine days later a 22 member band ("M27") began a series of 10 attacks on the remnants of "B26", which lasted a month. After the second attack a band male remained within the troop and subsequently defended it against further attacks by the, now 21 strong, band "M27". During associations between "M27" and "B26", band males and the new resident were injured and six of the seven females mated with the 'bachelor' males. During the period of band attacks four infants disappeared. Two were seen to be killed by biting by the new resident and another died 40 minutes after having been seized by the male and dropped from a tree (biting was not recorded). The fourth infant went missing in unknown circumstances. No females without infants were seen to be attacked (Mohnot 1971a,Boggess 1979). A fifth infant, probably sired by the new male, disappeared six and a half months later. Mohnot (1971a) presumes that it was killed by the new resident. However, apart from a tendency for the mother to avoid the male after parturition and appear 'afraid', there seems little evidence to attribute its loss to infanticide, no more so than the disappearance of the fourth infant.

The four infant-deprived females came into estrus within 1, 5, 9 and 11 days after infant loss. The females without infants at takeover also came into estrus concurrently. Six females copulated with band males and two with the new resident but the infant-deprived females did not give birth until, on average 17 months after takeover. It is therefore most likely that the new resident fathered post-takeover births (Mohnot 1971a).

Detailed information is also available for two other Jodhpur takeovers. A seven member band attacked the adjacent troops "Kaga A" and "Kaga B" and the adult male of each disappeared (Makwana 1979). The troops temporarily fused and females consorted with and solicited band males. The two troops were next observed separate, each with a new resident, which frequently chased away the five member band. The new "Kaga A" male had been troop male two years previously, but the following day a further new male was resident. That evening three infants were missing and the following day a one year old male was found to be injured. The latter animal was seen two days later in a band. Within the following month three more infants were found bearing wounds. The new residents threatened and chased infant-bearing females in both troops but disappearances and injuries only occurred in "Kaga A"; "Kaga B" retained its immatures. In the two months following takeover copulations between troops were noted but there is no published information on the timing or paternity of any subsequent births. Makwana & Advani (1981) report that two months after the fusion of "SH" and "SC" troops into the unimale "SH+SC" the original "SC" male was replaced by another. Tabulated data suggest that infant-loss did not occur. Information on a further four takeovers listed in

Makwana & Advani (1981) are not available.

The fusion of "SH" and "SC" is regarded here as a 'merging takeover' resulting from the disappearance of the "SH" resident male. Initially, both troops foraged together but separated for the night, the "SC" male invariably sleeping with that troop. After about a month the troops fused, with the "SC" male as resident and no evidence of infant disappearance.

In a 'divisive takeover' a six member band attacked the unimale "Ficus" troop and absorbed 6-8 adult females, one sub-adult female and their offspring (Makwana & Advani 1981). This new multimale was later reduced to unimale and the remnants of "Ficus" were 'supposed to have shifted elsewhere'. Therefore in seven social changes observed or inferred at Jodhpur, post-takeover attacks on infants were noted for two takeovers and seven infants disappeared. Three of these (all "B26") were observed to be killed by the new resident.

Mount Abu:Rajathan.

Hrdy (1974, 1977b) has carried out a long term (1971-75) study of langurs in and about the town of Abu by annual 1.5-3 month visits. Hrdy monitored the structure of seven troops, of which six were consistently unimale, and their relations with bands. Nine sudden social changes were recorded and a number of shifts in adult male membership; on occasion extra-troop males coexisted within troops and band-troop contact increased in the mating season. Of the nine changes eight are here classed as 'takeover' and one a 'divisive takeover'. In the latter case the "Toad Rock" troop divided into two unimale groups, one with the original resident and the other with an invader of unknown source. Two infant bearing females transfered to the invaders troop from the original residents' troop. The invader attacked and superficially wounded one of the infants, but neither disappeared.

The remaining social changes concerned "B3" and "B6", documented in Hrdy (1977b) and summarized in Boggess (1979) and Schubert (1982). These changes were largely inferred from compositition changes with apparently only one occurring during the presence of the observer. All but one of the changes involved three known adult males, with three "B3" takeovers occurring when the resident of "B6" vacated and entered "B3" (Boggess 1979). Four "B6" takeovers appeared to be the result of invasions after the residents departure from "B3". On one occasion "B6" was taken over and the resident temporarily became an extra-troop male. Two males tried to merge "B6" and "B3" but both failed. A total of 17 infants went missing shortly after takeover, five from two takeovers of "B3" and twelve from four changes in "B6". Between 1971 and 1974 83 % of "B6" infants disappeared. This probably represents mortality as it is unlikely that an infant could survive independently of a lactating female. Hrdy (1977b) attributes these losses to infanticide by invading males. However, the information on the cause of infant death is equivocal. According to Boggess (1979) nine of the seventeen infants went missing while Hrdy was absent from the study site. Of these nine, local inhabitants saw two or three killed by langur males. Of the remaining eight, which went missing while Hrdy was present, local people observed three deaths, again killed by langur males, but the circumstances of five cases were unknown. Hrdy witnessed attacks by invading males on three infants which resulted in wounding but never observed an assault which is known to have resulted in infanticide. After the takeover of "B3" by Righty, Hrdy observed approximately fifty assaults on infant-bearing females but none disappeared or were injured.

The temporal correlation of takeovers with missing infants, observed attacks and reports from locals suggest that infanticide by invading males did occur at Abu, despite Hrdy's non-observance of it. Such killing seems especially likely to have occurred in the Shifty 1971 "B6", Righty 1975 "B3" takeovers (Boggess 1979). More circumstantial evidence suggests its occurrence in April 1972 "B3", June 1972 "B6" and February 1973 "B6" changes.

Because of the intermittent nature of the observations little information is available on the paternity of either missing infants or of post-takeover births. Boggess (1979) concluded, after reviewing the Abu data, that although sexual activity increased immediately post-takeover, in six out of the seven birth intervals known for infant-deprived females, the interval was similar to that in which the pre-interval infant survived to weaning. In one case the birth interval was curtailed from some 20-30 months to 12 months by infant loss. Hrdy (1977b) estimated that the average male troop tenure at Abu was 27.6 months.

In addition to these three sites, Ripley (pers.comm. in Hrdy 1979) at Polonnaruwa and Starin (1978) at Gir have noted takeover-associated infant loss. Pathasarathy & Rahaman (1974) claim according to Angst & Thomen (1977,p200) that 'three infants were killed by the new leader male within a month after the takeover'. No further details are known to me. Hrdy (1979) also records a personal communication of infanticide in langurs at Sariska. Owing to the absence of any further information these four cases have been ignored in this chapter.

6.5.3 BAND-TROOP ASSOCIATIONS.

Laws & Vonder Haar Laws (1984) revealed a social organisation in the Indian Siwaliks at Rajaji which appeared to differ substantially from both gradual and rapid patterns of male replacement. Solitaries immigrated into the multimale troop, especially during the non-mating season. However, the authors obtained evidence that band-troop associations occurred during the pronounced monsoon mating season. Males attempting to enter the troop found higher resistance from the resident males during the non-mating season than the mating season. Immigrations were gradual, preceded by 'tracking' (similar to 'haunting' of Hrdy 1977 ?) and troop-band relations were characterised by low levels of aggression. The associating band males were about as successful as the residents in obtaining reproductive access to females. This pattern would appear to be, in essence, the opposite of the seasonal pattern in male membership changes found at Junbesi. It is however uncertain from the Laws' ten month study whether the band-troop associations were truly seasonal.

In summary, three major patterns of social change can be identified in Hanuman langurs: gradual male replacement, rapid male replacement (takeovers) and band-troop associations. Some 22 takeovers have been described, ten of which were accompanied by infant disappearance. Three infants were seen to be killed by the invading male and there is some evidence that birth intervals for infant-deprived females are shorter than for those females whose infants survive to weaning (see 6.4.2). Such violent episodes have not been recorded in populations with gradual male replacement or band-troop associations. In the former males tended to be excluded during the mating season, whilst in the latter, extra-troop males associated with a troop during this period. The reduction of multimale to unimale has frequently been observed at takeover sites. Female transfer between troops has very rarely been recorded; this sex class tend to remain in their natal troop. How can variability in male replacement patterns and the occurrence of infanticide be explained ?

6.6 HYPOTHESES OF SOCIAL CHANGE AND INFANTICIDE.

There has been considerable debate and heated controversy surrounding explanations for the variability in social change, and in particular infanticide, described in the previous section. For example, Schubert (1982,p201) regards one hypothesis (sexual selection) as 'a myth of our contemporary academic culture rather than (to be) a scientific fact'.

Two main, exclusive hypotheses have been proposed to explain the observation of infanticide:

a) Infanticide associated with takeovers is an adaptive male strategy evolved through sexual selection.

b) Infanticide is a maladaptive,pathological behaviour resulting from human influence on langur populations.

6.6.1 SEXUAL SELECTION HYPOTHESIS.

Sugiyama (1967) suggested, after observing post-takeover infant wounding and disappearance, that invading males killed infants in order to bring the mothers into physiological estrus sooner than if the infant survived to weaning. Hence, the new male resident would be able to sire offspring quicker and make more reproductive use of its short tenure. Trivers (1972) views langur infanticide as an extreme product of sexual selection and one of the rare occasions among mammals were inter-male competition persists after fertilization. Hrdy (1974,1977a,b) has developed this hypothesis into a model in which infanticide is seen as an adaptive strategy by the invading male, accelerating its access to females at the expense of former resident males, the infant deprived females and the infants.

Hrdy (1977b) suggests that, in situations in which males have brief tenure of reproductive access, it will be to the invaders

evolutionary advantage to kill infants sired by the previous resident as :
1) the invader reduces the reproductive success of the dead infant's father,relative to his own.
2) the invader eliminates individuals which may compete with its own offspring for food resources and, when mature, for mates.
3) infanticide curtails lactational amenorrhoea, accelerating return of the infant-deprived female to ovulation, and hence shortens the interval between takeover and birth of the invader's offspring.

The unweaned infants are obstacles to the male maximizing reproductive opportunities and a non-infanticidal male would be expected to leave fewer offspring. The three essential components of the hypothesis are that the invading male should not kill its own offspring but should sire and accelerate post-takeover births. Hrdy (1977b) suggests that the invading male can judge non-paternity of infants on the basis of previous consort relationships with the mother. Killing of own offspring or the offspring of relatives would be detrimental (unless parental manipulation, Hrdy 1979). If males disperse large distances relative to females (as appears to be the case;Hrdy 1977b) between spells of troop tenure and from the natal troop the probability of encountering related offspring will be low. However, particularly in island-type populations, males may be able to determine non-paternity from the identity of the mother and lack of matings with her in the last six months. As noted by Hrdy (1977b) conscious intent is not imputed, but only that males exhibiting advantageous behaviour will tend to be disproportionately represented in the next generation. Additionally, invariance is not to be expected, as mistakes will occur and behaviour should be considered in terms of probabilities.

The first two advantages of infanticide (above) would be expected to hold whatever the population characteristics. They have been little investigated but may have less effect on male reproductive success than the shortening of birth intervals. Hrdy (1977b) has proposed a related model of cyclical social change. In the initial stage, an extra-troop male engineers a takeover and kills infants. During the growth stage females produce his offspring and troop size increases. In the subsequent mature stage an age-graded multimale arises by maturation which may persist, be reduced to unimale or return to the initial stage by takeover. In areas of frequent takeover, troops would be expected to be predominantly unimale as troops lack the opportunity to 'mature' into the age-graded state (Curtin 1977,Hrdy 1977a).

Chapman & Hausfater (1979) have theoretically explored the sexual selection hypothesis by modelling the advantage to infanticidal and non-infanticidal males under varying demographic conditions. The model suggests that when infanticidal males arise in an otherwise tolerant population, infant killing will always be advantageous to males and will spread. However, once fixed in the population infanticide will only be advantageous, in comparison to non-infanticidal males, at certain tenure lengths. They predict that infanticide will be advantagous at ranges or 'windows' of tenure length of 4-7, 20-31, 41-53 and 62-76 months inclusive. Outside of these windows a non-infanticidal male will have higher reproductive success. This result arises because at such tenure lengths an infanticidal male's offspring would be unweaned at the subsequent takeover and hence vulnerable, whilst a non-infanticidal's young will be born after takeover (post-takeover births are not attacked). The quantitative predictions will depend on variables such as the inter-conception interval, as the shorter the amenorrhoea, the smaller the advantage conferred on infanticidal males. Therefore, rapid weaning would be expected to decrease the effectiveness of infant-killing. Chapman & Hausfater (1979) also show that the predicted tenure lengths in infanticidal populations, albeit crude, are consistent with field data. They suggest that, dependent on the distribution of tenure lengths, a population may be entirely infanticidal or adopt a mixed evolutionarily stable strategy or behavioural polymorphism, either between animals or within the life history of the individual.

Hausfater et al (1982) further explore this suggestion by modelling the equilibrium proportion of infanticidal males predicted at a given set of reproductive and demographic conditions. They demonstrate that once arisen, infanticide is unlikely to be lost except through chance. They predict that the equilibrium proportions of infanticidal males would be expected to vary in a cyclic manner with increased length of male tenure. The model also suggests that variation in one month of the estimated tenure can lead to a 97 % difference in the frequency of the alternative strategies. If the first two advantages of infanticide as listed above are overlaid on this model, the windows in tenure length at which infant killing would be advantageous may be increased in breadth (see Fig.4 of Chapman & Hausfater 1979). Therefore, these models have been useful in identifying the more pertinent variables and making falsifiable quantitative predictions.

Inter-sexual selection, or the favouring of male traits attractive to females, may also be involved. It is predicted (Hrdy 1977b) that although an infanticidal male may have killed a female's infant, the female should mate with that male, as by doing so she will produce (assuming it is a heritable trait) successful infanticidal sons. Therefore females may be in a 'cruel bind' in favouring matings with the male which destroyed her infant.

6.6.2 SOCIAL PATHOLOGY HYPOTHESIS.

The major alternative hypothesis seeking to explain infanticide has been developed by Curtin (1977), Dolhinow (1977), Curtin & Dolhinow (1978a) and Boggess (1979). It proposes that the unimale troop structure and takeovers are an abnormal social organisation resulting from a failure of the multimale structure to 'endure environmental conditions far different from those in which it evolved' (Curtin & Dolhinow 1978a;p475). The proposers note that unimale structure and infanticide have only been found at sites with high langur and human density in degraded habitats, with few predators. Crowding is supposed to have resulted from a concentrated human population drastically altering the habitat by deforestation, provisioning, creation of crop raiding opportunities and the destruction of predators. This degradation is regarded as recent, producing an environment very different from that in which the species evolved. Under such excessively unnatural conditions it is suggested that normal social relations break down, resulting in a disturbed population which exhibits aberrant, maladaptive behaviour such as infanticide. The death of vulnerable infants is the incidental result of escalated aggression among mature animals. It is therefore unnecessary to over-complicate the issue by attributing an evolutionary history and invoking evolutionary explanations for deranged behaviour, devoid of adaptive value. Langurs living in 'natural' environments have peaceful intra-group relations, which are transformed into social pathology under human influence.

6.6.3 OTHER HYPOTHESES.

Sugiyama (1965a) noted that infanticide has the effect of curtailing population growth at high density. Rudran (1973) suggested, for Presbytis senex, that takeovers and infanticide regulate the population and maintain the unimale structure. He proposed that the frequency of takeovers and infanticide is higher at high density and thereby maintains the population in balance with its resources. Hausfater & Vogel (1982) suggested that this hypothesis is also applicable to Hanuman langurs. Hrdy (1977b) however, noted that if infanticide is advantageous to individual males, population regulation, if it occurs, is a consequence and not an explanation for its evolution. If infanticide were not beneficial to the individual actor then its evolution as a regulatory mechanism would require group selection (Wynne-Edwards 1962). The social system in langurs is highly unlikely to meet the restrictive conditions under which group selection could act by overriding individual or gene selection (Maynard-Smith 1976). Therefore it would seem unlikely that infanticide has arisen to regulate populations, but by being more frequent with increasing density, it may well be a consequence.

Sugiyama (1965a), noted that infant-deprived females quickly returned to estrus and suggested that this provided an opportunity for the invader to consort with the female and establish social bonds to solidify his leadership. However, if this 'social bonding' hypothesis explains the adaptive significance of infanticide we would expect the evolution of female counter-strategies against such a disastrous imposition. Such strategies may be very difficult to evolve against males selected by Hrdy's (1977b) hypothesis. However, I would have expected the evolution of effective counter-strategies against such a strategy by promoting social bonding while still bearing an infant, perhaps by showing pseudoestrus.

Mohnot (1971a) suggested that the invading male kills because it experiences simultaneous sexual frustration and rage; the 'mixed emotions' hypothesis of Hausfater & Vogel (1982). However as this appears to be addressing causation and not function (Krebs & Davies 1978) it does not address the question, considered here, as to 'why' infanticide occurs.

6.6.4. DISCUSSION.

Of five proposed hypotheses seeking to expain infanticide, two appear to be viable candidates. These hypotheses were suggested in the light of the observations summarized in 6.5. However, there has been considerable debate as to whether the published evidence supports the sexual selection or the social pathology hypothesis. In this section the two models will be discussed with a view to coming to a conclusion as to which hypothesis is most consistent with the observations.

Hrdy (1977b) observes 'Only among hanuman langurs, however, is there sufficient information to say that infanticide occurs regularly, and under conditions that must now be considered normal for this species because these conditions are both widespread and of long duration ' (p246) and 'at Abu infanticide constituted the single greatest cause of mortality' (p65). Hrdy correlates the male invasions of troops with the disappearance of 39 infants at Abu, Dharwar and Jodhpur and attributes these losses to infanticide by the invaders. However, Schubert (1982), Boggess (1979) and Curtin & Dolhinow (1978a) dispute this conclusion, noting the paucity of unequivocal observations of langur infanticide and doubt whether it is a regular or normal event. Infants can and do go missing for reasons, such as disease, predators and falls, unconnected with takeovers. Feral 'pie' dogs and jackals, probably important predators of older infants, cause wounds similar to those inflicted by a male langur. Given the inability of primatologists to watch even one troop all the time and the sudden, brief and infrequent nature of the event it is not surprising that information on infanticide is equivocal in interpretation.

Infanticide has only been observed three times, all at one site, There is, however, strong circumstantial evidence, discussed in 6.5

for infanticide at Abu and Dharwar. The lack of information makes it very difficult to judge its frequency and which, if any, of the 36 other infants missing after takeovers were killed by invaders.

Apart from the these doubts as to the occurrence of infanticide Schubert (1982), Boggess (1979), Curtin & Dolhinow (1978a) claim, contrary to Hrdy (1977b), that the data that are accepted does not support the sexual selection model and that the social pathology hypothesis is the most parsimonious explanation. Hausfater (1977) commented that the absence of infanticide in certain habitats does not necessarily constitute evidence that it does or does not occur in other populations. Similarly, observation of infanticide in certain populations does not imply that it is a typical langur phenomena. The debate as to whether infanticide is 'normal' behaviour, is in this regard, rather uninteresting given the great variabilty langurs show in other aspects of their biology. The possibilty of both hypotheses being correct at different localities or that infanticide exists as a mixed ESS also suggest that an 'all or nothing' approach to its distribution may be incorrect. Here some of the major points made against each hypothesis and the counter-arguments will be discussed. More detailed discussions will be found in Boggess (1979), Schubert (1982), Hrdy (1977a,b,1979,1982), Hausfater & Vogel (1982), Curtin (1977) and Curtin & Dolhinow (1978a,b).

Curtin & Dolhinow (1978a) noted that infanticide has only been observed in high density populations, subject to pernicious human disturbance and never in conditions similar to those in which langurs evolved. In contrast 'normal' (i.e. gradual male replacement in multimale troops) social organisation has been recorded in habitats ranging from undisturbed forest to farmland. Hrdy (1977b) disputed the claim that human disturbed habitats are stressful or recent and suggests that langurs prosper in close contact with man and have done so for thousands of years.

Hrdy also suggests that the absence of takeovers from low density sites reflects its low frequency of occurrence in such populations and not normality versus abnormality.

Boggess (1979) and Schubert (1982) claim that there is considerable variation in the circumstances surrounding takeovers and infant disappearance. Takeovers lump a variety of patterns, including the invasion by bands, troops or solitaries, into troops without a resident male, unimale or multimale troops, resulting in multimale or unimale troops. Similarly, the circumstances surrounding infant death are variable, occurring both after male stability and during band-troop conflict. It is therefore unreasonable to explain such variety by a single functional cause and social pathology is the more reasonable explanation. However, it can also be argued that the variability observed is less than would be expected if chaotic, pathological behaviour was occurring. Although takeover patterns are variable, infanticide has only been observed when extra-troop males invade a troop. This restriction of infant killing to specific circumstances supports a predictable, functional explanation (Hrdy 1977b).

Similarly, the social pathology hypothesis predicts that although the more vulnerable immatures would be expected to suffer disproportionately, all age/sex classes would be injured in chaotic aggression. Curtin & Dolhinow (1978a) suggest that infants are killed as an incidental result of aggression among mature animals. However, injuries to animals, other than the adult males and young infants, have rarely been reported and the descriptions of attacks supports the contention that the infants are the targets (Mohnot 1971a,Sugiyama 1965a,b, Hrdy 1977b). Infanticide has been the only langur behaviour suggested as pathological; by analogy with rats (Calhoun 1962) if social mechanisms were to break down a variety of deranged behaviours would be expected.

Critics of the sexual selection hypothesis have also disputed its three essential components. In particular Schubert (1982), Curtin & Dolhinow (1978a) questioned whether invading males are able to discriminate paternity of infants. Dolhinow (1977) suggested that its recognition attributed incredible powers of memory and reason to langur males. However, determination of non-paternity may not be necessary if males disperse larger distances than females between residencies and from the natal troop. If, however, males repeatedly re-enter troops, as at Abu, it does not seem unreasonable to suggest that langur males can recognise females as individuals and whether they mated within the last year. Hrdy (1977b), in suggesting that it is the mother's identity that is the cue, notes that kidnapped infants from adjacent troops, although alien, are not attacked. As Boggess (1979) noted, there is insufficient field evidence for or against a paternity determination ability.

Additionally, infanticide may not substantially shorten the birth interval (Curtin & Dolhinow 1978a, Schubert 1982). Shortened birth intervals have been recorded in 11 out of 20 cases (Boggess 1979). With a mean interval for infant-deprived females of 17 months the Jodhpur data is particularily inconsistent with Hrdy's hypothesis. It is possible that inter-site differences in length of lactational amennorrhoea may be linked to the distribution of infanticide (Hausfater et al 1982). The field data is equivocal but would be amenable to testing in captivity.

Finally, it is often unclear, with copulations occurring between troop females and band males, during and after takeover, as to whether the new resident did inseminate the harem females (Schubert 1982,Curtin & Dolhinow 1978a). According to Boggess (1979) there is clear evidence of five infants being fathered by infanticidal males but in three times as many cases paternity is uncertain. Therefore, as above, field evidence is equivocal.

In conclusion, it is not possible to state in any confidence, from the extant literature, whether observations of langurs support the sexual selection or the social pathology hypothesis. Much of the evidence is circumstantial and equivocal in interpretation. The confinement of infanticide to high density populations living in close association with man, argues for the social pathology model. In contrast, the restriction of infanticide to specific circumstances argues for the sexual selection hypothesis.

The sexual selection hypothesis will prove very difficult to test, because of the difficulties of carrying out field experiments (Hrdy 1982). Its validity can, perhaps, best be tested by investigating individual components such as birth interval shortening and paternity discrimination, in captivity. The social pathology hypothesis is, however, more open to falsification as it is an essential prediction that infanticide will not be observed in undisturbed, low or moderate langur density habitats. Direct evidence of takeover-associated infanticide at such a site would argue for the refutation of the social pathology hypothesis for that population and yield circumstantial evidence that it is also untenable at Dharwar, Jodhpur and Abu (Curtin & Dolhinow 1978a).

PLATE 7

FIVE "Q" BAND MALES AT CARCASE OF INFANT-ONE # 18 (arrowed) OF "C" TROOP,SHORTLY AFTER INFANTICIDE. 19 APRIL 1981,QUADRAT 12/9.From a transparency.

PLATE 8

ADULT FEMALE # 29 OF "C" TROOP COPULATING WITH ADULT MALE # 24 OF "Q" BAND,QUADRAT 14/12. 13.20 hrs 30 April 1981. TWO SUB-ADULT FEMALES ON LEFT & RIGHT

CHAPTER 6.7 SOCIAL CHANGE AND INFANTICIDE. EVIDENCE FROM KANHA.

In this section changes in the social organisation of four Kanha langur troops are described and discussed with reference to the hypotheses detailed in 6.6.

6.7.1 OBSERVATIONS.

A/ "L" Troop: Multimale Phase & Male Replacement.

"L" troop occupied a block of forest to the east of "C", with whose range they slightly overlapped (see 8.3.3). When first observed "L" was a unimale troop (see Fig 6.19).

Between 18 July and 1 October 1981 "L" became multimale; comprising, in an incomplete census, of at least 5 adult males with ten adult females but no infants. At least four adult males appeared to have entered the troop during the monsoon; an adult female marker individual was present before and after the change. Whether the female or immature composition changed is not known as the troop was not completely censused until April 1982. This multimale state persisted until between 18 November and 16 January when "L" became unimale by the shedding of nine or ten males. The new adult male AM^{57}, was not seen during the previous unimale period, but was one of the males present during the multimale phase. Ten adult females were still present and during March and April there were three births, probably conceived during September. This structure persisted until 15 April 1982, when observations ceased.

Therefore a unimale troop went through some four months as a multimale troop and the adult male was replaced in unknown circumstances. Whether changes in membership of other age/sex classes occurred is also not known.

B/ "A" Troop :Loss of Sub-adult Males.

"A" troop, which overlapped the western boundary of "C"'s range (see 8.3.3), remained unimale from May 1980 until May 1983. Three censuses, carried out in three successive years at the same season are given below:

April 1981	:AM-1,AF-11,S-5,J-3,IN2-3,IN1-2	25
April 1982	:AM-1,AF-11,SM-5,SF-3,JM-1,JF-4,IN2-1,IN1-8	34
April 1983	:AM-1,AF-10,SF-5,J-8,IN1-3	27

The composition differences between April in 1981 and 1982 are probably the result of births, although without complete individual identification other changes cannot be excluded. Between 1982 and 1983 "A" had a net loss of an adult female, five sub-adult males and one individual of unknown category. The adult male of "A" did not change from 1981 to 1983.

Therefore "A" appeared to have, over two years, a relatively stable composition, with the loss of an adult female and five sub-adult males.

C/ "B" and "C" troops:transfer of females.

"B" troop was observed from 25 February until 27 June in 1980. In early May 1980 "B" consisted of 28 langurs (see Fig 6.20). By early June this was reduced to 26 with the presumed death of AF^3 (see 6.4.3) owing to the non-delivery of a still-born infant and the disappearance of AF^1, presumed dead or emigrated.

On 18 June, "C" troop, which had not been observed before, was sighted in the study area (see Fig 6.20). This group was composed of three adult males, AF^5 of "B" with two other adult females, a juvenile female, a juvenile of unknown sex and an infant-two; nine animals in all. Concurrently "B" was reduced in size and was missing AF^5. By 27 June "C" had increased to sixteen langurs by the addition of three adult females and four animals of unknown category. On the 28 June, "B" had lost nine langurs: six adult females, three infant-ones and two juveniles but had gained two infant-twos. It is possible that the changes in the latter two categories were the result of observer confusion between juvenile and infant-two descriptions. "B" lost one marker individual (AF^5) but retained four. One of the three adult males of "B" (AM^2) lacked a nose septum and appeared to be the same individual as a band male sighted on the meadows on 1 March 1980. If this origin is correct, then a third group must have been involved as the juvenile female in "C" could not have been derived from either "B" or a band. A five member band was observed 'haunting' (see Hrdy 1977b) "B" on seven days in May; so it is possible that the males were derived from this band. Because of the low proportion of identified animals in "B", it is not possible to be confident as to "C"'s origins. Although it seems likely that it was formed in June 1980, all or part of it could have migrated from elsewhere. The fate of missing "B" animals, which did not appear in "C" is also unknown.

With such sketchy information one can only speculate that the simplest re-organization that would result in the observed outcomes is that "B", a band and a troop interacted in un-observed events resulting in the formation of "C". Whatever the details, the important feature of this social change is the transfer of an adult female from a unimale troop into a multimale. After this change "B" occupied the SE corner of the grid and "C" the central and eastern areas about Kuloo chattan, with about 50 % inter-troop range overlap.

On my returning to the area in January 1981 both troops were found in the same ranges. Five marker individuals were relocated. During my absence "B" had become multimale and lost two adult females leaving a predominantly male troop. The change to multimale could have resulted from a male invasion but is more simply explained by the maturation of sub-adult males. In contrast, "C" had become unimale, losing two adult males and an animal of unknown category. The adult male of "C" was AM^{23}, AM^{2} having disappeared. It is not known if AM^{23} was one of the three original males of "C". "C" and "B" were involved in eleven observed encounters from February to April, with a rate of 0.5 per day.

On 19 April 1981, AF^{22} with its presumed daughter $IN2^{25}$ transferred from "B" to "C". On the 21 April AF^{11} transferred likewise (see Fig 6.20), resulting in "B" losing all its females to become an all-male band, renamed "R". As a result, "C" troop increased to fifteen animals, four of whom at least were previously in "B". In mid-June 1981 "R" increased to fourteen animals with the addition of three males. "R" ranged considerably more widely than "B" had done, occupying an area at least from the southern area of the grid to the Desi/Churi nullah confluence (see Fig 6.3) The last sighting of "R" was on 28 July 1981. The transfer of females from "B" to "C" occurred during attacks by "Q" on "C" which resulted in infanticide and a takeover (see next section) During the two weeks following the transfer of $AF^{11,22}$, they were frequently harassed and displaced by other adult and sub-adult females of "C".

It is speculated that the simplest scheme of interpretation is that "C" was formed in 1980 from part of "B", a band and another troop. In 1981 the three remaining "B" females transfered to "C" resulting in the formation of a band ("R") by fission.

D/ "C" Troop takeover and infanticide by "Q" band.

During April and May 1981 "C", as well as gaining three "B" females, was involved in a series of encounters with the all-male band "Q". These began with the killing of three infants by "Q" males in mid-April. After a period of consorting between "C" females and "Q", AM^{23} was replaced by AM[30] of "Q". The daily events are summarized from field notes in Appendix IV and changes in composition are tabulated in Appendix V.B. Relations between "Q"-"C" during April and May 1981 are diagramatically summarized in Fig.6.21 and in the following text, with observations divided into three phases on the basis of the type of interaction. See also Plates 1, 7 and 8.

On the 18 April (Phase 1), during an 85 minute encounter a "C" infant (IN1[17]) was seen to be mortally wounded by invading "Q" males. The infant was seen to be bitten in two bouts and also fell some 20 m from a tree, resulting in the penetration of its cranium and injuries to the thorax and abdomen with protruding intestines. It died some 2.5 hours after the first injuries and was finally abandoned within 3.5 hours of its death. Its mother was probably AF[28] (the uncertainty arises because of incomplete troop identification early in the study). "Q" band, which had not been seen before, departed without any change in adult membership; AM[23] remained as "C" male. Adult females without infants were not observed to be chased apart from one occasion when they intervened in an arboreal chase. A sub-group of about three large adult males of the 13 member band were largely responsible for the chasing of females; the smaller adult and sub-adult males were involved in interactions with AM[23]. The whereabouts of the "C" male were unknown for the majority of the encounter, although he was not present in the vicinity of the infanticide. After a brief period of chasing and counterchasing at the onset of the conflict, it was lost from view. During the encounter "C" was inconspicuous and hard to locate, harder than when resting arboreally. "Q" males frequently gazed into the canopy as though searching which, given the context, is likely to have been for infant-bearing females.

On the 19 April, during a "Q"-"C" encounter lasting in excess of three hours, IN1[18] was seen to be killed by "Q" males (see

Plates 1, 7). IN1^{18} weighed 1.46 kg. and is preserved in the Forest Department Museum at Kanha F.V. It is illustrated in Plate 1 and had extensive deep penetration wounds to the thorax and thighs consistent with being inflicted with canines. As on the 18 April AM^{23}, was not present during the actual infanticide and did not intervene during the chase. Only the large "Q" adult males were involved and again chases were strikingly directed with only infant-bearing females being attacked. The infant, which probably died within a minute, was abandoned by the adult female on it being snatched by the "Q" males. The killing occurred 150 m from the rest of the troop and the adult female, whose identity is not known, fled.

On the 20 April, during a 1.7 hour encounter between "Q" (now 16 males) and "C", the band males did not come into close proximity to infant-bearing females. With the arrival of the band, "C" polarized, infant-bearing females fleeing to a stream whilst two sub-adult females approached them, squealing. Five large "Q" males also progressed to the stream but "C" females appeared to be in concealment. "Q" was supplanted from proximity to infants by AM^{23} and "B" males opposing the band concurrently.

On 21 April, IN1^{19} died during a three hour "Q"-"C" encounter. Although not actually witnessed (contact was lost for 60s) the circumstances strongly suggest that, especially if the events of 18 and 20 April are taken into account, IN1^{19} was bitten to death by the "Q" males. The only alternative, in the observed absence of a third party, is that the carrying female killed the infant, probably its own offspring. The polarization of "C", with infant-bearing females fleeing to concealment and sub-adult females approaching "Q", was again evident. The recently immigrated female bearing an infant two was attacked and the infant was later noted with an injury. AM^{23} was ineffectual in discouraging attacks. The adult female, probably AF^{29}, carrying IN1^{19} at the onset of the attack did not abandon the carcase until 205 minutes after its, probably instant, death.

In summary, during Phase 1, four encounters with "Q" resulted in the death of three "C" troop infants (a male, 6-8 weeks old; a female,2 weeks old; one unsexed, 6-8 weeks old). The actual killing of two, by "Q" males was clearly observed. The killing of the third was missed by some 30-60 seconds but the circumstances strongly suggested infanticide by "Q". It is not known whether the dead were AM^{23}'s offspring. AM^{23} was ineffectual in preventing attacks. "Q" males only initiated attacks on infant-bearing females which fled into apparent concealment. No animal older than an infant was observed with wounds.

During Phase 2 (Fig 6.21,Appendix III,IV), "C" formed sub-groups, rejoining at night, with 'AM23' and infant-bearing females remaining separate (100-500m) from "Q" whilst the remaining females consorted with the band. Two adult females mated with AM24 (see Plate 8) and solicitations, rarely observed in the month prior to band invasion, were common. The band attacked the infant-bearing sub-group once during this period and one female carrying an infant eluded pursuing males and AM^{23} supplanted "Q". "Q" was not recorded within the study area on five days.

With the replacement of 'AM23' by a "Q" male 'AM30' (Phase 3, Fig 6.21,Appendix III), polarization ended and frequent attacks by 'AM30' on infant-bearing females began, which subsided in June. In late May, when attacks were diminished, the frequency of violent adult male-female interactions during 12 days of dawn to dusk observations was 2.83/day ± s.d. 2.12. Females intervened in 68 % of 31 such attacks for which there are data. The frequency of these conflicts declined to 1.67/day in June and 0.42/day in July. Frequency of occurrence of these male assaults on 138 complete days, spread equally across the year, was

0.61/day ± s.d. 1.16. The new resident was rarely observed to chase females without infants; such chases were mostly of females which intervened in assaults on infant-bearing females. The circumstances of the male replacement were not observed, AM23 was last seen with "C" on the morning of 5 May, but by the afternoon it had disappeared and AM30 (without "Q") was troop male. AM23 was never seen again. During the period of takeover the six month old infant-two was attacked, but despite serious wounds survived; no infant disappeared. From mid-May "C" troop had occasional agonistic encounters with band "Q" and no band-"C" female consorting occurred. Frequency of solicitations and copulations declined after takeover but increased considerably during the late monsoon (see 6.4.1). In the subsequent birth season ten infants were born which, assuming a 200 day gestation (Hrdy 1977b) suggests that first conceptions occurred in late May. This indicates that 'AM30' was most likely the sire. Between August and October two infants, born pre-takeover, disappeared in unknown circumstances and 'AM30' remained "C" resident, at least until May 1983. "Q" was last observed with all marker individuals present on 29 July 1981.

In the following discussion these observations are considered with reference to the two infanticide hypotheses (see 6.6.); are they consistent with the sexual selection hypothesis, the social pathology hypothesis, both or neither ?

6.7.2 DISCUSSION OF KANHA OBSERVATIONS.

In this section, firstly the non-infanticidal social changes and secondly the "C" change involving infanticide are discussed and compared with observations of other langur populations.

B/ Non-infanticidal social changes.

"A" troop composition was relatively stable, with the only major change the loss of five sub-adult males, probably by emigration. It is possible that the "A" adult male expelled the younger males to prevent the unimale troop becoming a multimale, or the males may have left because the chances of reproductive success elsewhere, by takeover or mating with adulterers, may have been higher than remaining. Mohnot (1978) has documented the former process.

The four month spell "L" spent as a multimale (probably not age-graded) resulted in male replacement. No infants were present at the change to multimale and it is uncertain as to whether the subsequent births were conceived when uni- or multimale. The "L" change is similar to that reported for Jodhpur, in which troop male changes were frequently characterised by 2-4 months as a multimale (Vogel 1979). It may also be likened to the pattern of gradual male replacement (Boggess 1979) but, if the multimale structure was present during the monsoon mating season, the pattern may be more akin to band-troop associations (Laws & Vonder Haar Laws 1984).

"B" troop gradually reduced in size, mainly by shedding females, until transformed into the band "R". Four, and possibly more of these females, transfered to "C" at its probable establishment and also a year later. The probable formation of "C" is similar to the interpretations of the Dharwar "40" and "5" divisive takeovers. The reduction of multimale to unimale, as occurred to "C" during the observer's absence has been frequently recorded. The transfer of females between troops is unusual however with the majority of females probably spending their entire lives in the natal troop. With the transformation of "B" into the band "R" it, as is typical for bands, ranged over a much wider area than that occupied by "B" (Chapter 8). This troop to band transmutation by female emigration does not appear to have been previously recorded in langurs. There were no elements of takeover, as the "C" male was never seen to contest 'ownership' of the "B" harem with "B" males; the change appeared to be endogenous. The adult sex ratio before the change was 11:2 which suggests that perhaps the males split from the females (the adult females were both old and hence of low reproductive value, Hrdy 1977b) to seek greater reproductive opportunities elsewhere as a band. Owing to the probable genetic relationships within troops (Hrdy 1977b), it is likely that $AF^{11,22}$ were more closely related to AF^{5} and perhaps other "C", originally "B", langurs than animals in other adjacent troops. The proximity of kin may therefore have influenced the direction of female transfer. The probable high degree of relatedness among "R" males, may also, by kin selection, have important consequences for inter-male behaviour, especially during takeover.

The timing of female transfer is suprising considering that an unweaned infant was placed in the context in which two young infants had just been killed. The attacks and wounds on $IN2^{25}$ suggested that it did emigrate into a dangerous situation. It is possible that if the males initiated breakup of "B", the females had no choice and the difficulties of entry into troops without kin and the dangers of living as an isolate, necessitated entry into "C".

Therefore, of four troops monitored only one did not show changes in adult male composition. A great variety of changes are thought to have occured with female transfer, troop to band transformation, divisive takeover, multimale reduction, immature male emigration, gradual male replacement with multimale phase (or troop-band association) and takeover. The occurrence of the latter two patterns at the same site indicates that the suggested dichotomy between sites into those with rapid and those with gradual male replacement (Hrdy 1977b,Curtin & Dolhinow 1978a) may not be valid; it is probable that both rapid and gradual male replacement occur at the same site with different populations having a preponderance of one type or a mixture of patterns. The variation observed in Kanha also suggests that many studies are far too short to conclude what pattern of social change, if any, is typical; even after a two year study little insight is obtained as to the frequency of occurrence of the different types of group inter-change.

B/ Discussion of takeover and infanticide.

The rapid male replacement in "C" was in many respects similar to takeovers observed at Dharwar, Jodhpur and Abu. In the following sections the details of the "C" takeover will be discussed and interpreted in relation to the two alternative hypotheses purporting to explain langur infanticide.

1/ Kanha as a test of the social pathology hypothesis.

As discussed in 6.3, langur density in Kanha is at $46/km^2$ moderate within a species range of $2-133/km^2$ (Hrdy 1977b). In view of the richness of the habitat, with high arboreal primary production, it is unlikely that the Kanha density is abnormally high in relation to the environment. Furthermore, the Kanha habitat is not, at present, heavily influenced by human activities; indeed, along with other central Indian forest populations, they are probably one of the least disturbed in peninsula India. Kanha meadow langurs are not provisioned, cannot crop raid, rarely come into close contact with people and live 1.5 km from the nearest village. Habitat alteration has occurred (see Chapter 3), with selective felling some eighty years ago and Baiga slash and burn cultivation. It is argued in 6.3.3. that the creation of the meadow is likely to have reduced, rather than increased, density. The sal forest is probably as similar as any other extant Indian forest to the environment in which the Hanuman evolved.

Therefore the direct observation of takeover-associated infanticide is of significance in relation to the sexual selection-social pathology debate. As noted by Curtin & Dolhinow (1978b) in the context of the social pathology hypothesis :

"Our argument can be refuted by the observation of infanticide in undisturbed habitats at low or moderate population densities." (p669).

The Kanha observations are therefore clear evidence that this hypothesis cannot be supported at this site; the contention that infanticide is the aberrant, incidental result of escalated aggression resulting from compression of langur populations, is untenable in Kanha. If the hypothesis is unacceptable for Kanha, it does suggest the possibility that it is also unlikely to be valid at Abu, Jodhpur and Dharwar. Evidence against the social pathology hypothesis in one population does not however, necessarily prove or imply support for the sexual selection hypothesis. Indeed, infanticide cannot be regarded as any more 'normal' behaviour than the gradual male replacement observed by Boggess (1979). It is this variability in pattern of social change which requires explanation (Hausfater 1977).

In the following seven sections the "C" takeover will be discussed in roughly chronological order.

2/ Pre-takeover infanticide.

In comparison with observations in the literature and with Hrdy's (1977b) hypothetical scheme the most striking difference of the

Kanha takeover-associated infanticide is the reversal in the sequence of events, with infanticide followed some 15 days later by a takeover. Approximately similar patterns have been occasionally reported. In the B6 1973 Abu takeover (Hrdy 1977b) an infant was injured by a band, a member of which later replaced the troop male. During the troop "30" takeover at Dharwar two of the five infants disappeared whilst male membership changes where still occurring and the "B26" troop infanticide at Jodhpur occurred after takeover but during repeated aggressive band encounters. However, although much of the information is incomplete, it does appear that most observed and inferred infanticide has occurred after takeover. Pre-takeover infanticide is not inconsistent with the sexual selection hypothesis. If a male or its kin kills infants and then takes over, the essential element of the hypothesis is not violated. Pre-takeover infanticide may erode the advantage to the resident of staying as troop male and hence perhaps accelerate takeover and increase the probability of a successful band invasion. Faced with an infanticidal attack a single resident would, by staying, incur the risk of serious injury. If females fail to effectively protect infants from invaders the resident's optimal strategy may be to desert, terminating investment, and try again elsewhere. Resident male strategy may depend on such probabilities as of future reproductive success elsewhere (not past investment; Dawkins & Carlisle 1976), of defeating the band, of being injured in an escalated fight and of being the father of the infants. Whether post- or pre-takeover occurs may depend on resident and invader 'assessments' of ability and intentions and of the probability of infanticide occurring in the presence or absence of the band males and troop male. The hypothesis may, for example, predict that younger residents would desert sooner than older males as the latter, with lower reproductive potential, would be expected to invest more in the aggressive countering of invaders than young males (Clutton-Brock & Harvey 1976,1977).

3/ The circumstances of infanticide.

The three cases of takeover-associated infanticide from Kanha doubles the tally of langur infant killing, observed by zoologists, to six. AM^{23} was ineffectual in preventing these assaults but it remained as resident throughout the attacks. Of the five "Q" chases of infant-bearing females three resulted in infant death and AM^{23} intervened twice. The intervention of AM^{23} on behalf of $IN2^{25}$ (on April 21) was surprising in terms of the sexual selection hypothesis as it would seem very unlikely to have been its offspring. Indeed, if AM^{23} had remained resident, the sexual selection hypothesis would have predicted attacks by this male on the infant. Females were also ineffectual in defending infants against attacks, as is witnessed by "Q"'s high success rate, either when carrying or in intervening. Intervention by females against males may have had a very low probability of success in the two cases of male coursing of lone infant-bearing females across open meadow. Indeed, the only case of intervention was in the arboreal chase on the 18 April which, in the restriction of the canopy, may have stood a higher chance of success. The youngest infant was killed first. This could have arisen by chance or perhaps because the infanticidal male has more to gain, in terms of shortening birth intervals, by killing the youngest offspring.§ Young infants may also be the most vulnerable to male attack.

I was very forcibly struck by the goal directed nature of the attacks during the infanticidal phase. The only aggression directed at non-infant bearing females was when they intervened in the arboreal chase. Despite three infant deaths and one wounded infant (injury sustained in unknown circumstances) no wounds were observed on any other "C" animal. The great difficulty I had in locating infant-bearing females in the presence of "Q", including their occurrence in sub-terranean stream beds,

§ Younger infants will delay the invader's reproduction longer than will older infants.

suggests deliberate concealment. By comparison, females without infants were easier to locate both in forest and meadow.

'Stotting' behaviour, in which "Q" males jumped high 'on the spot', similar to that shown in antelopes (Leuthold 1977), was twice observed when "Q" was close to obscured females with infants, and in no other context. The behaviour may therefore have been an attempt to gain height in order to locate females in long grass areas. The direction of "C" polarization on the two occas ions that "C" was aware of the approach of "Q", prior to the beginning of the encounter, also supports the contention that infants were the targets. Females gave low grunts, appeared agitated and whilst infant-bearing females fled, two sub-adult females approached the band. This direction of breakup was also observed in the second phase when diurnal sub-groups formed. There is therefore considerable evidence, albeit circumstantial and anecdotal, that attacks are not chaotic, but predictable and aimed at infants; females are incidentally involved as the carriers of young.

Half of the 1981 cohort of infants were killed by "Q" and with the subsequent disappearance of two others, only one or 16.7% of infants survived to weaning. There was no evidence of 'haunting' (Hrdy 1977b) prior to takeover as "Q" was first seen on the 18 April. On the 20 April three "B" males (to become "R" on the following day) acted concurrently with AM^{23} in supplanting "Q": perhaps "B" and "C" males acted in concert against "Q". This was the only day in Phase 1 when an infant was not killed. It is perhaps possible that "B"'s action may have been related to the recent immigration of $IN2^{25}$, which AM^{6} may have sired, into "C". It is speculated that "B", whose incursion into the centre of "C"'s range was tolerated by AM^{23}, was attempting to safeguard kin. AM^{23} only supplanted "Q" on one other occasion, on 30 April in Phase 2.

The observations suffered from three important deficiences.

Firstly, the precise identities of the infanticidal males are not known. AM^{24} was involved on one occasion but the whereabouts of AM^{30}, AM^{23}'s successor, during the attacks is unknown. Secondly, the identities of the mothers of two infanticide victims is not known with complete certainty and is not known in the third case. Thirdly, the paternity of infants killed is uncertain as they were conceived during the observer's absence (August & September 1980) when "C" may have been unimale or multimale and the whereabouts of AM^{23} were unknown. It is unlikely that any of the "Q" males were the father.

4/ Consorting and polarization.

The sub-group formation in Phase 2 appeared to have affected ranging behaviour; April was the most dissimilar month in terms of inter-monthly range overlap (see Chapter 8), probably as a result of the infant-bearing sub-group visiting the extreme south-west of the study area, which was never seen to be occupied by "C" again. Both sub-groups fused at night and "Q" slept apart from "C". Perhaps the polarization represents a dichotomy of interests between the two sub-groups with infant-bearing females remaining discrete from the potentially dangerous males, the resident remaining with them in an attempt to safeguard their young. Why, however, do unencumbered females consort ? Despite adulterous solicitation and copulations between $AF^{11,29}$ and AM^{24}, assuming a 200 day gestation, no conceptions can have resulted. The consorters could either have been in physiological estrus and failed to conceive or in pseudoestrus (see 6.4.1.) and deceiving "Q" males as to their true reproductive state. If the former occurred it may be because that females favour proven infanticidal mates above the eclipsed AM^{23} as, if the trait is heritable, she would produce successful infanticidal sons (Hrdy 1977b). Hypotheses, applicable if pseudoestrus was occurring, are discussed below.

5/ **The Takeover.**

Phase 3 began with the replacement of AM^{23} by AM^{30} and lasted until late June when adult female-male conflict subsided. AM^{30} was previously recorded in "Q" but nothing was observed to suggest as to why this male, among sixteen, should become the resident. AM^{24} and two other "Q" males were thought to have larger body size than AM^{30}. As bands have been little studied this is one of the least understood aspects of takeovers. Moore (1983) found that a large band consisted of two sub-groups, one of young and another of old males. When the band took over a troop the young sub-group expelled the old males.

6/ **Post-takeover births.**

No alien males were seen associating with "C" after mid-May and apart from the unsuccessful adultery of AF^{31} with AM^{L}, no other inter-group matings were observed. Assuming a 200 day gestation it is therefore likely that AM^{30} sired the cohort of ten infants born in the 1981/2 season. The probable mother of one of the dead infants (AF^{29}) unsuccessfully copulated with a "Q" male nine days after the infanticide. Hrdy (1977b) notes that a crucial element of the sexual selection hypothesis is that a female, if deprived of her infant, would give birth sooner than if the infant has survived to weaning. These birth intervals are calculated in 6.4.1. The comparison of the interval with and without infant loss, 11.7 ± s.d. 1.61 and 26.5 months respectively, suggests considerable acceleration of births subsequent to infant mortality, supporting Hrdy's hypothesis.

7/ **Female counter-strategies ?**

Hrdy (1977b), noting that infanticide must have a large detrimental effect on female lifetime reproductive success, suggests that females may have evolved counter-strategies to try to reduce their losses. Hrdy suggests that post-conception estrus associated with takeover is a female strategy to induce the male to tolerate her subsequent offspring. By mating whilst pregnant the female 'confuses' the male as to the paternity of post-takeover births thereby inducing the male to tolerate them. There have been no reported cases of killing of infants born after male replacement. For the hypothesis to be viable it is necessary that male should be unable to discriminate pseudo- from physiological estrus. The paternity confusion hypothesis is not supported by observations from Kanha as no female, assuming a 200 day gestation was pregnant at takeover. There was, therefore, no need for the females to confuse males as no births, conceived before male replacement, were expected.

Schubert (1982) suggested that pseudoestrus is not a counter-strategy but an appeasement behaviour by females to prevent male attacks on themselves. On only one occasion did a Kanha infant-bearing female ($AF^{22}IN2^{25}$) present to an attacking male. Curtin (1977) and Curtin & Dolhinow (1978a) suggest that estrus does not follow infant disappearance but the presence of strange males induces receptivity in females with older infants, and thereby promotes infanticide. Infant killing is regarded as an incidental consequence arising from the combination of newly estrus females with vulnerable infants and sexually active males. As infant-bearing females were not recorded as exhibiting estrus behaviour prior to attacks, or in any other context, the Kanha evidence does not support this hypothesis.

None of the above hypotheses appearsto fit the Kanha observations. It is possible that the soliciting of "Q" males by females without infants may have evolved as a 'distraction display' to forestall attacks on kin with infants. The unencumbered females may attract the 'dissatisfied' band males, dangerous to troop mates and their offspring, with their promiscuity by deceiving them that they are enjoying reproductive success and thereby preventing attacks on infants. This assumes, as does the paternity confusion hypothesis, that females are able to conceal their true reproductive state. Kin selection is invoked as troop females are thought to be highly related (Hrdy 1977b) and hence inclusive fitness may be increased by safeguarding related infants at little personal cost. There is insufficent evidence to confirm or refute this suggestion. If females have evolved such behaviour, males would be expected to be under intense selection pressure to overcome the females' deception.

Hrdy (1977b) also invokes kin selection or reciprocal altruism to propose that females cooperate in the defense of infants against infanticidal males. In Kanha the general non-intervention when opposing a band and intervention when facing a single male may be related to the probability of success i.e. the chances of deterring a band are very small but appreciable when opposing a lone male. The absence of known post-takeover infanticide may have been due to the violent female intervention thwarting attacks.

Hrdy (1977b) also suggests that pre-pubescent sexual solicitations by older female immatures may be an appeasement counter-strategy attempting to forestall attacks. The solicitations given towards AM^{30} by $IN2^{25}$ during the period it was being attacked are consistent with this hypothesis.

The advantage accruing to an infanticidal, relative to a non-infanticidal, male can be crudely modelled using data from "C" troop. In the lower part of Fig 6.22 the actual temporal distribution of post-takeover births is shown. If all females were to give birth again nine months after killing of the entire cohort, the birth pattern shown in the upper part of Fig 6.22 would be expected. Differences between observed and predicted result from survival of infants and variation in timing of post-infanticide conception. However, without infanticide, a considerably delayed birth pattern would be expected, as also shown in the upper part of Fig 6.22. Assuming a 27 month birth interval for the six infant-bearing females and a nine month birth delay for the five females without infant at takeover, the disadvantage to the non-infanticidal male is evident. If infanticide had not occurred, some infants would have been born soon after but over half would have been born fifteen months later than if the male had been infanticidal. The two "C" residents also probably had widely different reproductive success during their tenure: only one of six infants born born during AM^{23}'s tenure survived to weaning as opposed to seven out of ten born during during AM^{30}'s tenure (and a further two infants were still present but unweaned at the termination of the study).

Therefore, in conclusion, the occurrence of rapid and gradual male replacement in Kanha suggests that populations cannot be classified by this distinction. The restriction of injurious aggression by band invaders towards infants, the shortening of birth intervals and the new resident's probable siring of subsequent births supports the sexual selection model. Infanticide in an undisturbed, medium density langur population is at variance with the prediction of the social pathology hypothesis. Why, however, has infanticide associated with takeover been reported at only a restricted range of sites ? How does langur infanticide compare to the same phenomena in other mammals ? These two questions are considered in the final section of this chapter.

6.8 GENERAL DISCUSSION : INFANTICIDE.

6.8.1 INFANTICIDE IN MAMMALS.

Infanticide has been reported for a wide variety of mammals, but the variety of the circumstances suggest that a unitary hypothesis is unlikely to be appropriate (Hrdy 1979). Here, infanticide amongst other mammals will be briefly reviewed.

Most mammalian infanticide has been linked to the sexual selection hypothesis (Hrdy 1979,Hausfater & Hrdy in press). Amongst the colobines there is strong circumstantial evidence for its occurrence in purple-faced langurs, P.senex (Rudran 1973), silvered leaf monkeys, P.cristata (Wolf & Fleagle 1977), Kibale red colobus, C.badius (Struhsaker 1983) and perhaps in Tana red colobus (Marsh 1979) and black & white colobus, C.guereza (Oates 1977b). Among cercopithecines infanticide is known for the red tailed monkey, C.ascanius (Struhsaker 1977) and apparently baboons, Papio sp. and blue monkeys, C.mitis (references in Hrdy 1982). In all species of colobine, except red colobus, and in the red tailed monkey infanticide is thought to have occurred in association with the takeover of unimale troops and accounts appear to be consistent with the sexual selection hypothesis. The absence of cannibalism among colobines, but its occurrence among cercopithecines (red tailed monkeys, gorillas G.gorilla and chimps P.troglodytes), may reflect incompatability of mammalian flesh with the ruminant-like digestion of the former sub-family.

The report of infanticide in red colobus is particularly interesting as in the Kibale forest this species, atypically for a colobine, is patrilineal and organised in multimale troops. Infanticide would not be predicted in such species as a male would be likely to kill infants sired by another, probably closely related, troop male in their natal troop. However, the one case of infant-killing in twelve years of observations, by its unusual circumstances, does support the sexual selection hypothesis. This arises because the infanticidal male was, as the son of an immigrant female, not conceived in its natal group and hence unrelated to other males (Struhsaker 1983).

Presbytis senex, for which there is strong circumstantial evidence for infanticide, is organized in unimale troops, but has 'predominantly male troops', which include immature females instead of bands. Rudran (1973) estimated that the average male tenure in troops was 36 months and that only 40 % of unimale troops contained post-infant immatures. Hrdy (1977b) suggested that, as a result of short tenure, immature females are unlikely to reach menarche during a males residence and are therefore expelled as competitors.

Infanticide in gorillas (Fossey 1981,Hrdy 1977b) has similarities with langur observations but the intra- and inter-community killings in chimpanzees are not understood (Goodall 1977). Sekulic (1983) appears to invoke sexual selection in explaining infanticide in red howlers (Aloutta seniculus) which was associated with changes in the relative status among male residents and the entrance of new males into multimale troops.

The Serengeti lion (P.leo) has a similar social structure to langurs, with periodic invasions by male coalitions into matrilineal prides, and takeover-associated infanticide (Bertram 1975). Packer & Pusey (1983) have suggested that the observed pattern of high sexual activity but low fertility after a takeover may be advantageous by reducing the frequency of takeover-associated infanticide. They propose that heightened sexual activity increases inter-male competition and results in larger male coalitions becoming resident in the pride. These are more likely than smaller coalitions to remain in the pride, protecting cubs, until the young are reared. There is also strong circumstantial evidence for infanticide in tigers (H.S.Panwar pers.comm,S.& B.Breeden pers.comm.).

In captivity, controlled conditions have permitted the testing of aspects of the sexual selection hypothesis. Mallory & Brooks (1978) were able to show that strange males, but never fathers, frequently killed infants in collared lemmings (Dicrostonyx groenlandicus). Additionally, offspring of males who killed and then mated with the mother were born sooner than males which did not kill but did mate. These experiments therefore confirmed the ability of males of this species to judge paternity and shorten birth intervals, two essential components of the hypothesis. Mallory & Brooks also suggest that, if the probability of encountering strange males increases with density, infanticide may be an explanation for the population cycles in wild lemmings.

Two other adaptive hypotheses for infanticide have been proposed in which the killing is disadvantageous to the victims parents (Hrdy 1979). Firstly, infanticide may result from the exploitation of the infant as a resource, such as 'aunting to death' in langurs (Hrdy 1979) or cannibalism e.g. infanticide by young males in Belding's ground squirrels, Spermophilus beldingi(Sherman 1981). Secondly, it is possible that infant killing can result from competition for physical resources (Hrdy 1979). For example, Sherman (1981) proposed that infanticide by adult female Belding's ground squirrels may, as a result of intense intra-sexual competition for nest burrows safe from predators, function to eliminate nest-site competitors. He also suggested that territoriality in this species may be related to the defense of young from conspecifics.

In both the above examples and in the sexual selection hypothesis, infanticide is disadvantageous to the victim's parents. However, in certain circumstances, such as the birth of inappropriate or defective young, the 'parental manipulation hypothesis' (Hrdy 1979) suggests that infanticide may improve the mother's reproductive success by terminating disadvantageous investment. Dickemann (1979) found evidence that post-partum manipulation of sex ratios in humans (to the detriment of females) fitted this model. The 'Bruce effect' in captive pregnant mice, in which they reabsorb foetuses when exposed to strange males (Bruce 1960) may represent the termination of investment in offspring liable to be killed.

Infanticide, of no adaptive advantage to the killer animal, may also occur by accident. For example, in elephant seals (_Mirounga angustirostris_) high pup mortality, as a result of being squashed during inter-male conflicts, is associated with high population density at breeding sites (Sherman 1981).

6.8.2 DENSITY, SOCIAL CHANGE AND INFANTICIDE.

In comparison with some other well documented cases of infanticide, such as Belding's ground squirrel or lions (see 6.8.1), langurs are particulary interesting in showing considerable variation in its incidence (see 6.5), why ? In this section the distribution of infanticide between populations and in time will be discussed. Three explanations were proposed by Hrdy (1977b) to account for this intra-specfic variation.

A/ Genetic heterogeneity.

Hrdy (1979) suggested that the variable occurrence of infanticide may be the result of genetic dissimilarity between populations. Morphological variation does not, however, correlate with type of social change. Hrdy (1979) suggested that differences in social change between Himalayan and peninsular populations may be the result of genetic differences, as may be the case for other characters (Vogel 1973). However, if this was the case, it still begs the question as to why infanticide evolved in peninsular India and not in the Himalayas.

B/ Observation conditions.

Hrdy (1979) also suggested that the recorded variation may be an artefact arising from differences in observation conditions. In high density populations, observers have greater opportunity to monitor a number of different groups and, therefore, more social changes would be expected to be seen. Hrdy showed that the number of troop-months observed at sites without takeovers was $^1/15$ of that at sites with takeovers. Hrdy (1979) discounts this hypothesis by assuming similar takeover frequency between sites. However, if this frequency is related to density, some of the observed variation may be an artefact of observation conditions.

C/ Demography.

Rudran (1973), Hrdy (1977b,1979) suggested that infanticide and takeovers are associated with a restricted set of demographic conditions. Yoshiba (1968) and Hrdy (1979) proposed that takeover frequency is higher at high population density, irrespective of human influence. They suggested that at high density, high proportions of unimale troops and 'dissatisfied' extra-troop males occur in the vicinity of troops, resulting in a higher frequency of social change. Boggess (1979) suggested that inter-male dominance in multimale troops restricts the invading males access to troop females and immatures, thereby preventing infanticide. Such restrictions would not apply if the invading male found itself 'alone' with a unimale troop.

In Fig.6.4-12 langur study sites are plotted in relation to a number of pairs of population structure variables (see 6.3.3). The subset of intensive long term study sites are further subdivided, into those with takeovers (Abu, Dharwar, Jodhpur and Kanha), those showing gradual male replacement (Melemchi, Junbesi), troop-band associations (Rajaji) and equivocal social change (Orcha, Simla). Hrdy (1979) suggested

Gir and Polonnaruwa as takeover sites but, as Boggess (1979) claims them as gradual male replacement sites, they have not been included. Inspection of Figs 6.4-12 suggests a tendency for the four takeover sites to segregate out on the axes from other localities. Takeovers appear to be associated with high proportions of unimale troops and extra-troop males, large mean band size, imbalanced sex ratio and small range size. Although some other sites show similar values, they are not consistently clumped according to type of social change. The sample size for gradual male replacement is small but these sites consistently have values at the opposite extreme to takeover sites, for example showing low levels of unimale character and large range size. In Fig 6.9 it is evident that takeovers occur at a wide range of densities (18-100 km^2) and apart from a lack of takeovers at very low density (<$10km^2$) there is no clear relationship between density and pattern of social change. However, the relationship is complicated by the relatively abstract nature of density estimates across habitat types. The effect of density on langurs would be expected to depend on such aspects as the dispersion and abundance of resources; for example the density at Jodhpur may be, in effect, far higher than that implied by $18/km^2$ as resources are few and clumped in a harsh, arid environment.

Therefore, the data suggest that troop structure, particularly the number of adult males per troop, and not density is associated with type of social change. Perhaps there is a continuum from gradual to rapid social change, related to demography. Although the proportion of unimale troops and extra-troop males, which are inter-related (see Fig 6.4), may be important, it is not known whether they are a cause or an effect. The lack of understanding as to the functional significance of unimale and multimale structure aggravates the problem (see 6.3.3). One approach to the question of 'why ?' multimale may be to consider alternative male strategies (i.e. the costs and benefits to the resident of allowing other males to remain and to the supernumery males of remaining; Clutton-Brock & Harvey 1976,1977). For example it may be the better reproductive strategy for a male, if the probability of future matings in a multimale is low, to join a band and attempt takeovers or take advantage of adulterous solicitations.

D/The timing of takeover and infanticide.

If takeovers are part of an extra-troop male strategy to increase reproductive success, it is predicted that the optimal time for invading troops would be between birth and mating seasons. If invasion was to occur after the mating season the receptive females would probably have already been inseminated. As new residents do not kill post-takeover births (Hrdy 1977b) takeover before the birth season would result in a cohort of infants appearing at the onset of the male's tenancy, obstructing his reproductive access. The temporal distribution of takeover onset, from Table 6.D, relative to the birth season peak (defined as median of birth season in Fig 6.17 with the July & August lesser season at Abu ignored) is shown in Fig 6.23. The data agree with the predicted timing of takeover and provide strong circumstantial evidence for the phenomenon being an adaptive male strategy.

Therefore, in conclusion, infanticide has been proposed to occur for a variety of functional reasons, but its observation in lions, langurs and in some other primates is consistent with the sexual selection hypothesis. Variation between langur populations suggests that the distribution of infanticide is associated with aspects of troop structure, in particular with the number of adult males and not density. However, cause and effect cannot yet be disentangled. The timing of takeovers at all four langur infanticide sites agrees with that predicted if the behaviour is an adaptive male strategy.

6.9 LANGUR SOCIAL ORGANISATION AND INFANTICIDE : SUMMARY.

1/ The study troop "C" of individually recognised animals, and three adjacent troops were opportunistically monitored throughout fieldwork and the langur population in 7.8 km^2 of the Kanha maidan censused.

2/ Langur population density was 46.15/ km^2, consisting of 14 troops (13 unimale, 1 trimale) and 4 all-male bands. Mean troop size was 21.7, band size 14, troop adult sex ratio 1:7.9 and population adult sex ratio 1:2.5. Biomass was estimated at 385.96 kg/km^2. The hill population, although probably of lower density, had similar stucture.

3/ The Kanha population, in comparison with other Asian sites, had moderate langur density, troop and band size but had a very high preponderance of unimale troops and extra-troop males. The troop adult sex ratio was highly unbalanced. A review of published data suggests that unimale troop structure is associated with a high proportion of extra-troop males, large mean band size, unbalanced sex ratio. The functional significance of these associations is not understood.

4/ Sexual activity was highly seasonal, predominantly May to August. Gestation, estimated from field data was similar to the 200 days reported from captivity. Many females showed post-conception pseudoestrus. Inter-group matings were rare.

5/ Birth intervals for two females whose infants survived to weaning were 24 and 29 months. The mean birth intervals for five infant-deprived females was 11.7 months.

7/ "C" troop doubled in size during the study owing to prolific births and female immigration. Three infants were killed and five animals disappeared.

8 / Patterns of male social change reported in the literature are reviewed and classified as i) gradual introductions and exclusions ii) rapid adult

male replacement by 'takeover' and iii) band-troop associations. The circumstances of takeover-associated infanticide at Dharwar, Jodhpur and Abu are summarized.

9 / The two main hypotheses seeking to explain langur infanticide, the sexual selection and social pathology hypotheses, are described.

10/ The existing field evidence for and against each hypothesis is reviewed and concluded to be equivocal.

11/ "L" troop underwent a multimale phase resulting in adult male replacement. "A" troop lost five sub-adult males. "C" troop was probably formed in 1980 from members of a band, "B" troop and other unknown groups. In 1981 two adult females and a female infant-two transferred from "B" troop to "C" resulting in "B" becoming the band "R". A great variety of social change was found in Kanha with both rapid and gradual male replacement. It is suggested that the transfer of "B" females to "C" may have been influenced by the presence of kin in "C".

12/ In April 1981 a band "Q" repeatedly invaded "C" and killed three out of six infants. After a phase of consorting between band males and "C" females, AM^{23} was replaced as resident male by AM^{30} from "Q". After the takeover there were frequent adult male-female conflicts which lasted for two months.

13/ The recording of infanticide in Kanha increases the number of zoologist-observed langur infant killing to six. Its observation in a moderate density population in undisturbed forest is strong evidence against the social pathology hypothesis. The details of infanticide are consistent with the sexual selection hypothesis.

14/ Pre-takeover infanticide, the reverse of the usual sequence, may erode the advantage to the resident in remaining and thereby accelerate and increase the probability of a successful takeover. Aggression by "Q" was directed at infants; no other animals were injured. "C" tended to polarize in the presence of "Q", with infant-bearing females fleeing into apparent concealment. Some unencumbered females approached "Q". The resident male was ineffectual in preventing attacks. The precise identities of infanticidal males were not known, the maternity of two infants was probably known whereas the paternity of all three was unknown.

15/ In the two weeks following infanticide, on five days, "C" formed two sub-groups, reuniting at night. AM^{23} and infant-bearing females remained separate from "Q", whilst unencumbered females consorted with "Q", four of whom copulated with band males. In early May, AM^{23} was replaced by AM^{30} from "Q". AM^{30} attacked an infant-two and infant-bearing females, with intervention by other females.

16/ The essential components of the sexual selection hypothesis, that the invader should not kill own offspring but should sire and accelerate post-takeover conceptions are supported by Kanha data.

17/ Evidence of female counter-strategies against infanticidal males is equivocal.

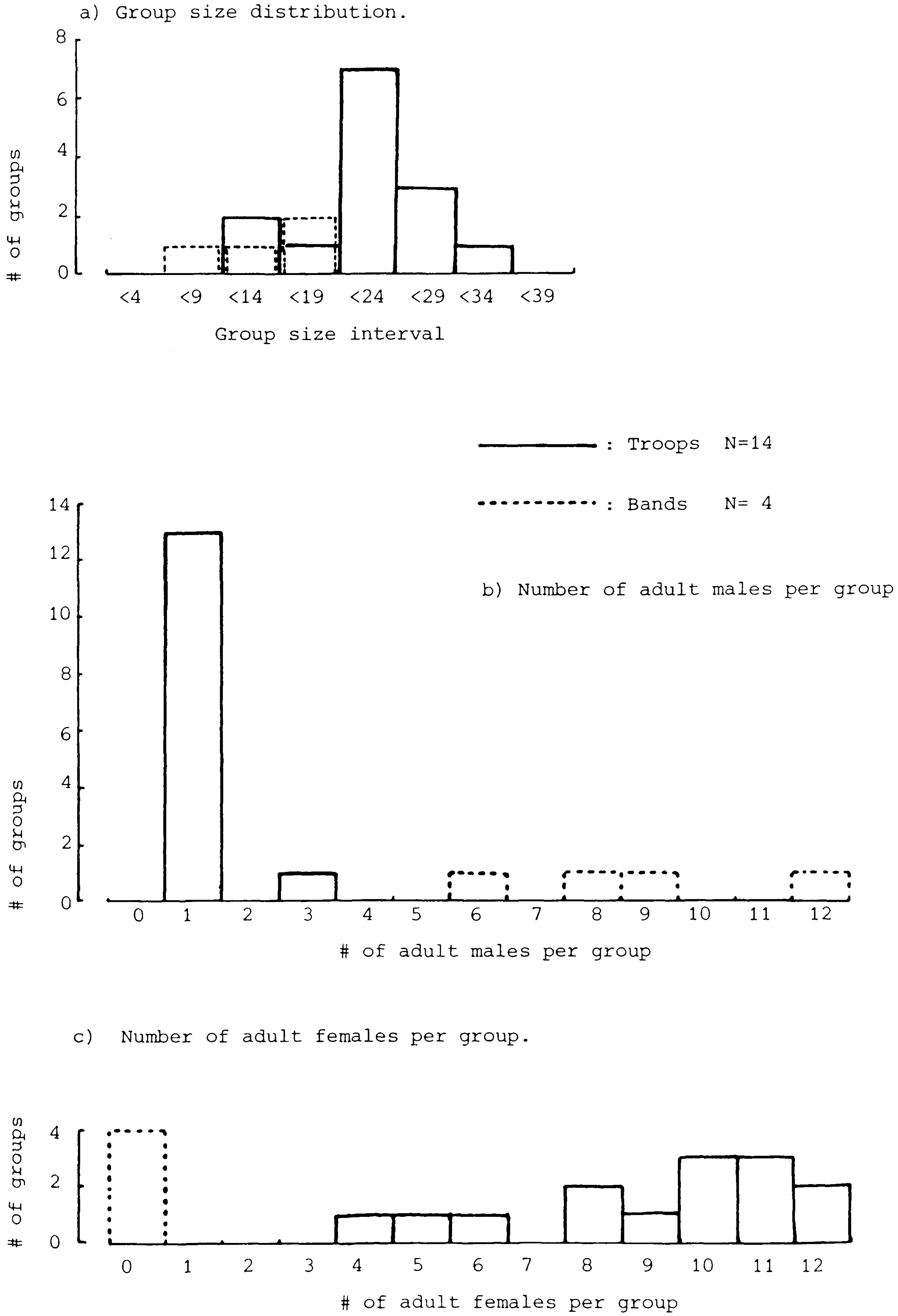
18/ Takeover-associated infanticide appears to be associated with troop structure, in particular the number of adult males per troop and not with density. Cause and effect cannot be disentangled.

19/ Infanticide in lions, lemmings and some cercopithecids is similar to the phenomenon in langurs and is consistent with the sexual selection hypothesis. Infanticide may have evolved for different reasons in other species.

20/ It is predicted, from the sexual selection model, that the optimal time for male invasion is between birth and mating seasons. There is good agreement between field data and the prediction.

FIG 6.1 LANGUR POPULATION STRUCTURE : KANHA MAIDAN.

(Data from April census).



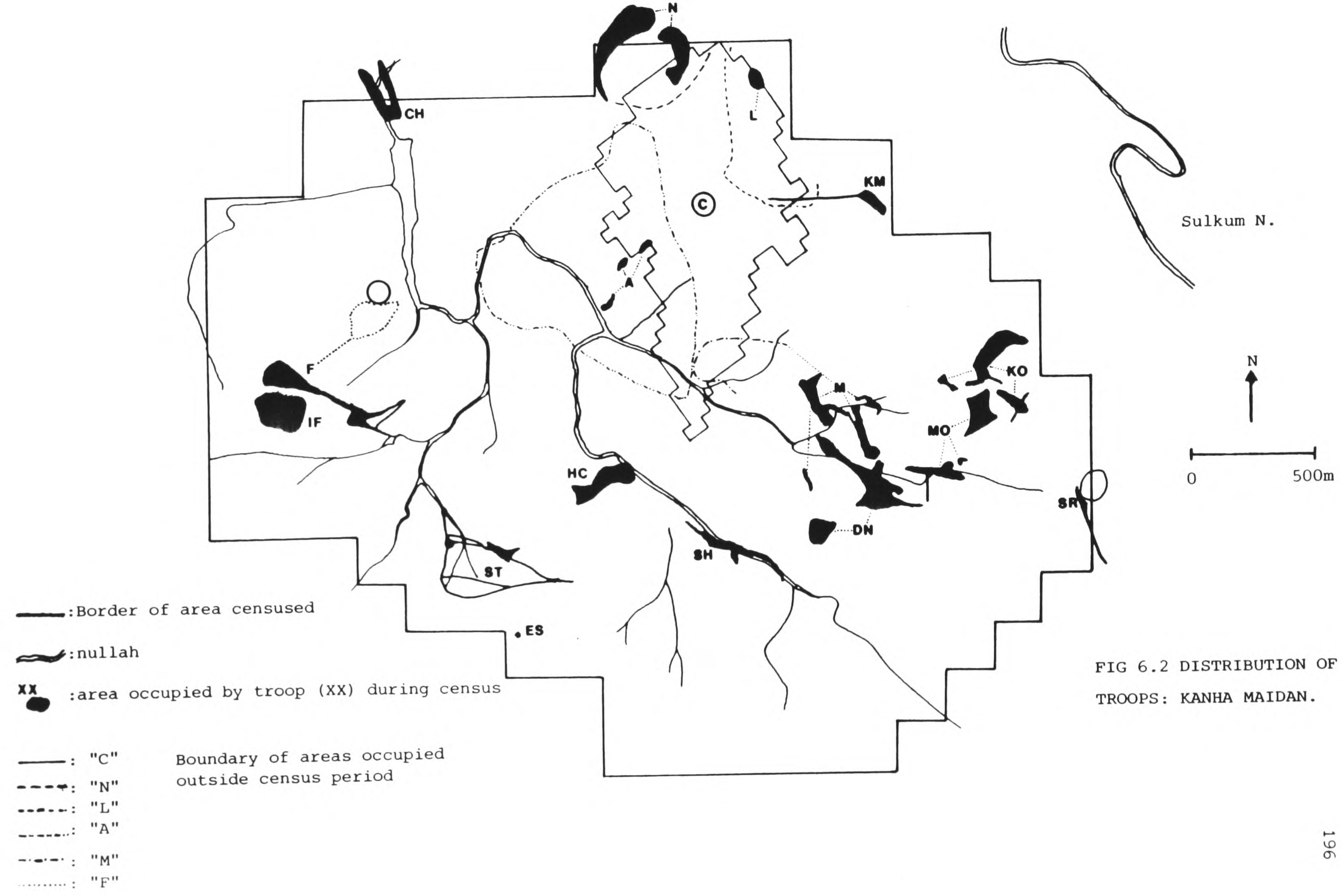


FIG 6.2 DISTRIBUTION OF TROOPS: KANHA MAIDAN.

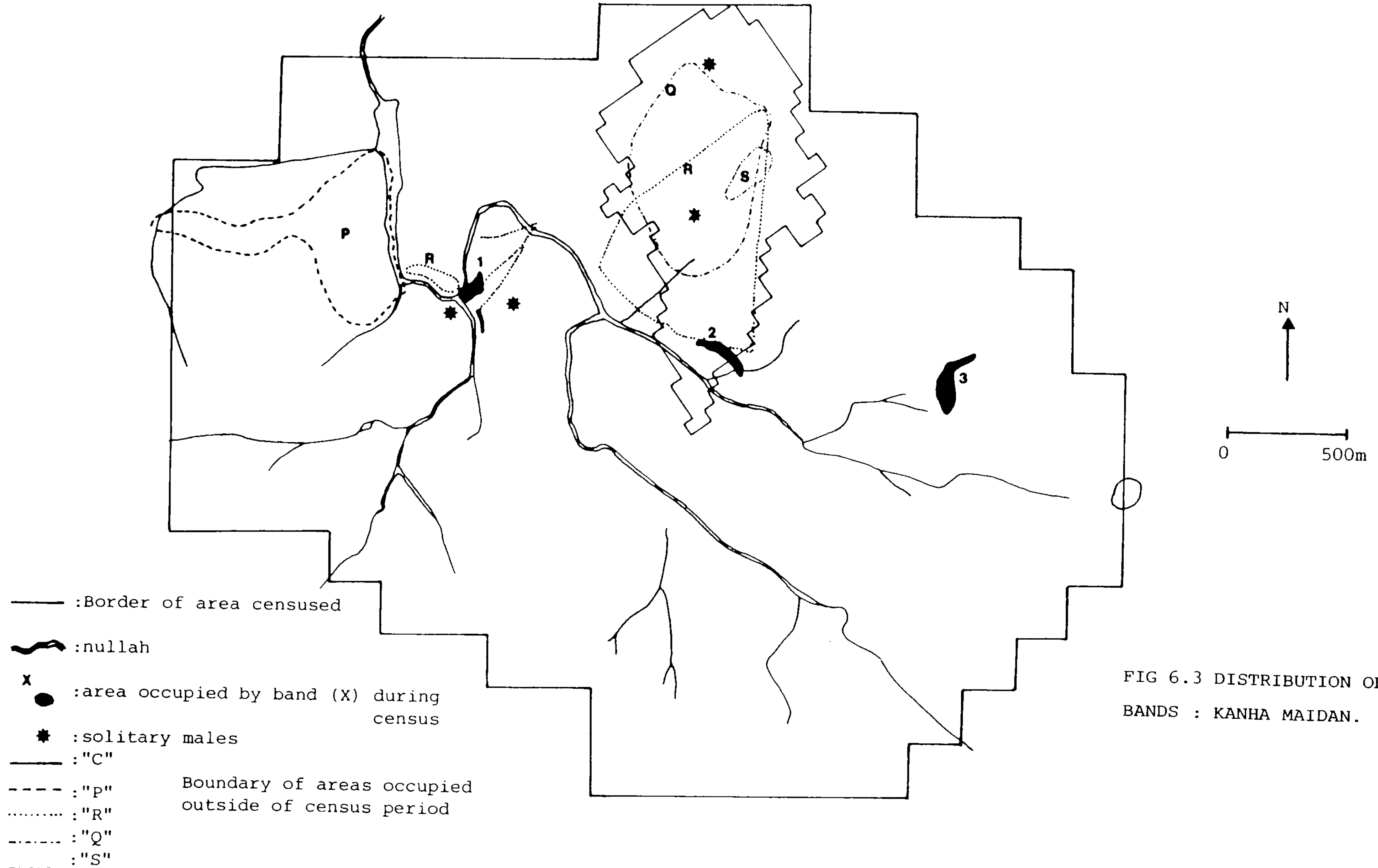


FIG 6.3 DISTRIBUTION OF BANDS : KANHA MAIDAN.

FIG 6.4 RELATIONSHIP BETWEEN % OF UNIMALE TROOPS AND % OF EXTRA-TROOP MALES. (see FIG 6.12 for symbols).

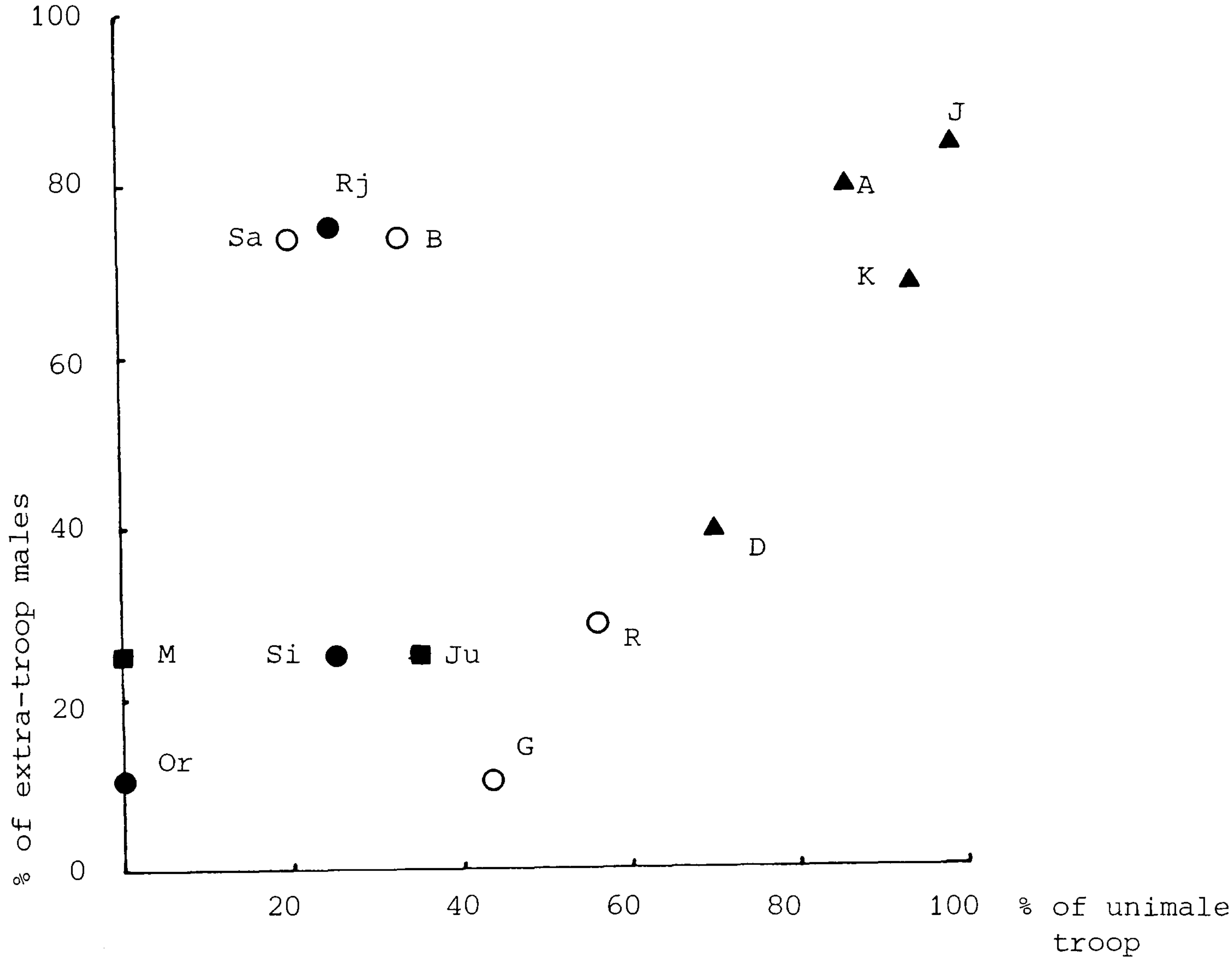


FIG 6.5 RELATIONSHIP BETWEEN % OF EXTRA-TROOP MALES AND TROOP ADULT SEX RATIO. (see FIG 6.12 for symbols). $r_s=0.759, p<0.05, y=1.48+0.05x, n=8$.

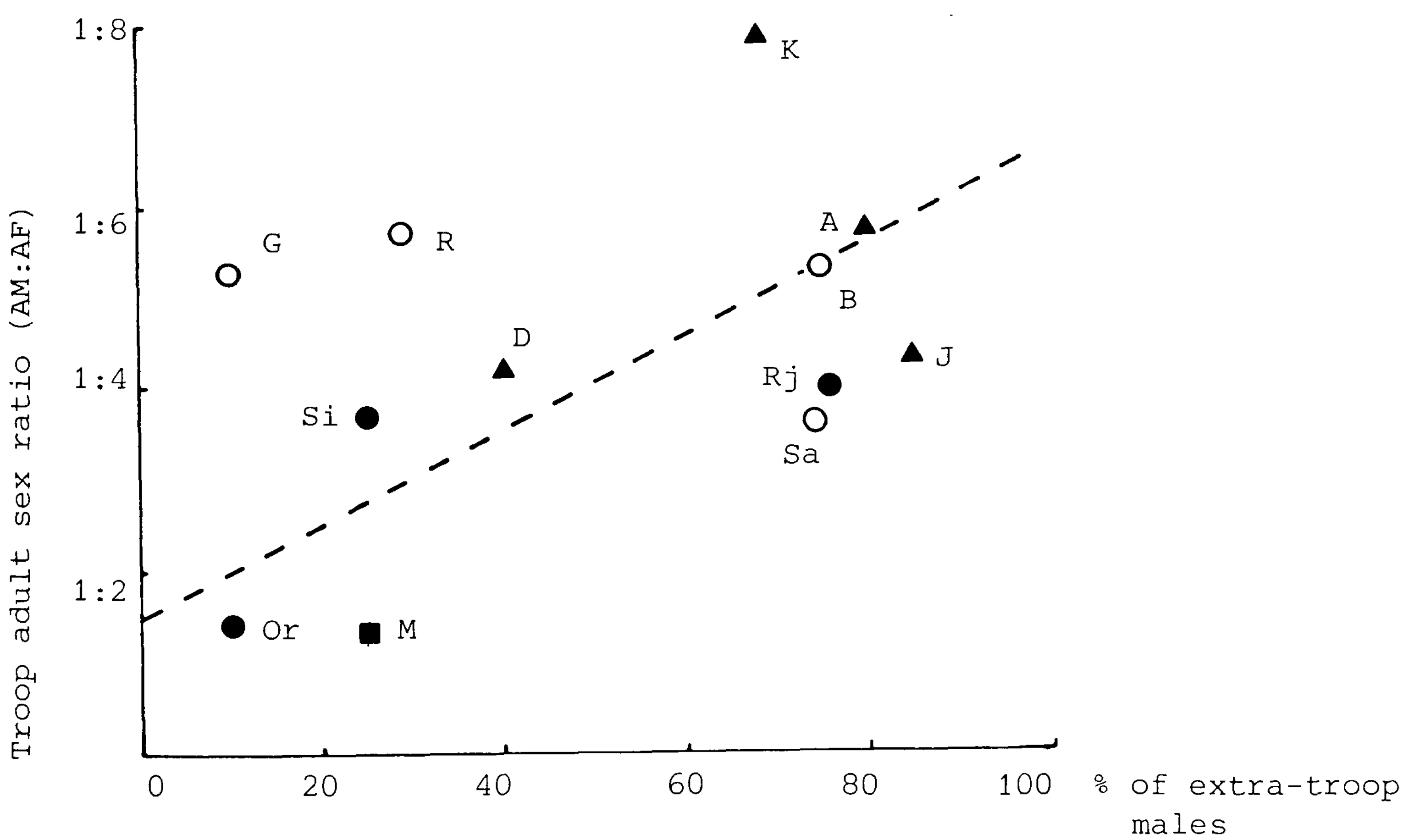


FIG 6.6 RELATIONSHIP BETWEEN % OF UNIMALE TROOPS AND TROOP ADULT SEX RATIO. (see FIG 6.12 for symbols), $r_s=0.924, p<0.01, y=1.93+0.04x, n=8$.

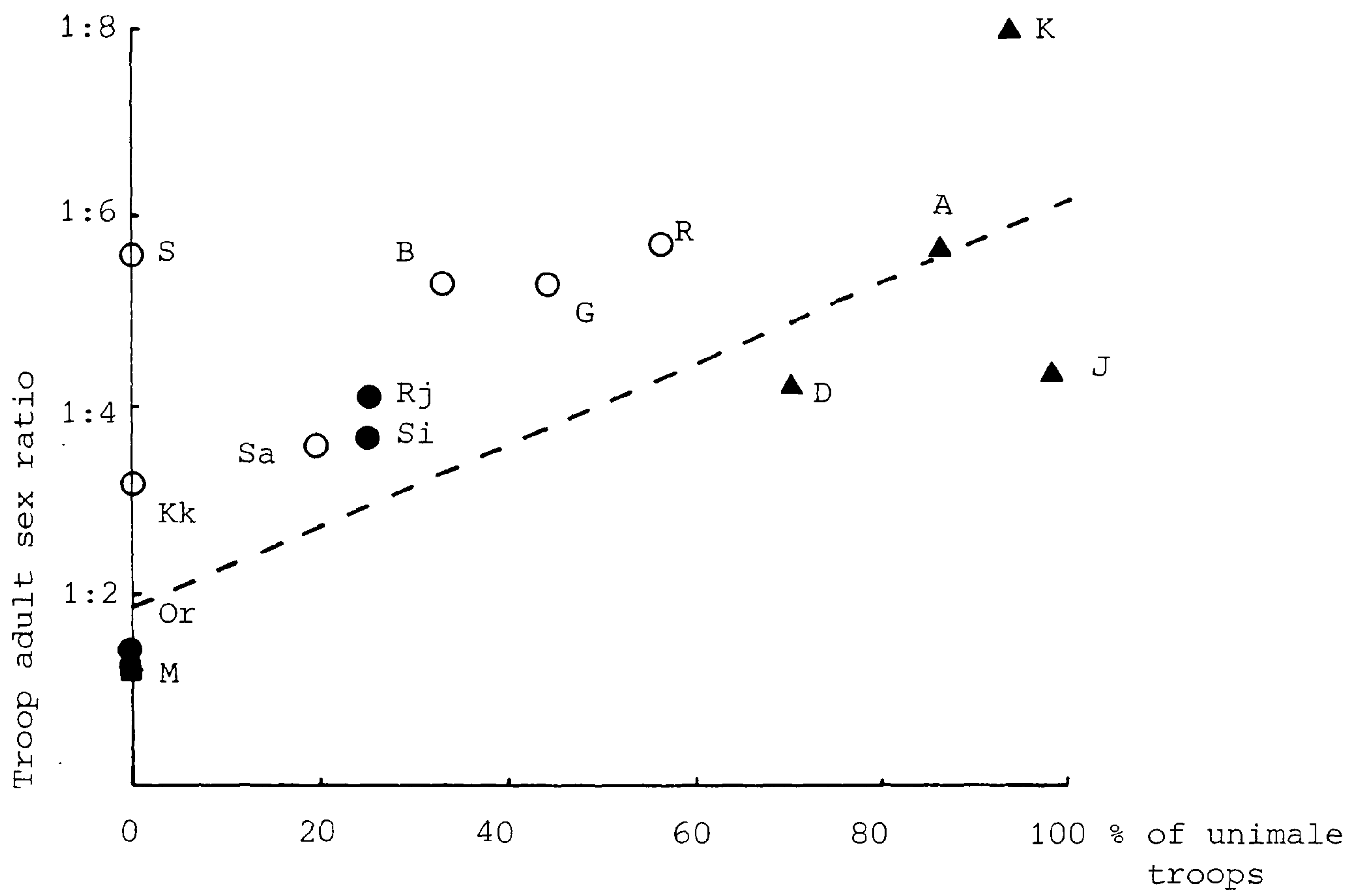


FIG 6.7 RELATIONSHIP BETWEEN % OF UNIMALE TROOPS AND BAND SIZE. (see FIG 6.12 for symbols) $r_s=0.814, p<0.01, n=10$, $y=0.740+0.121x$.

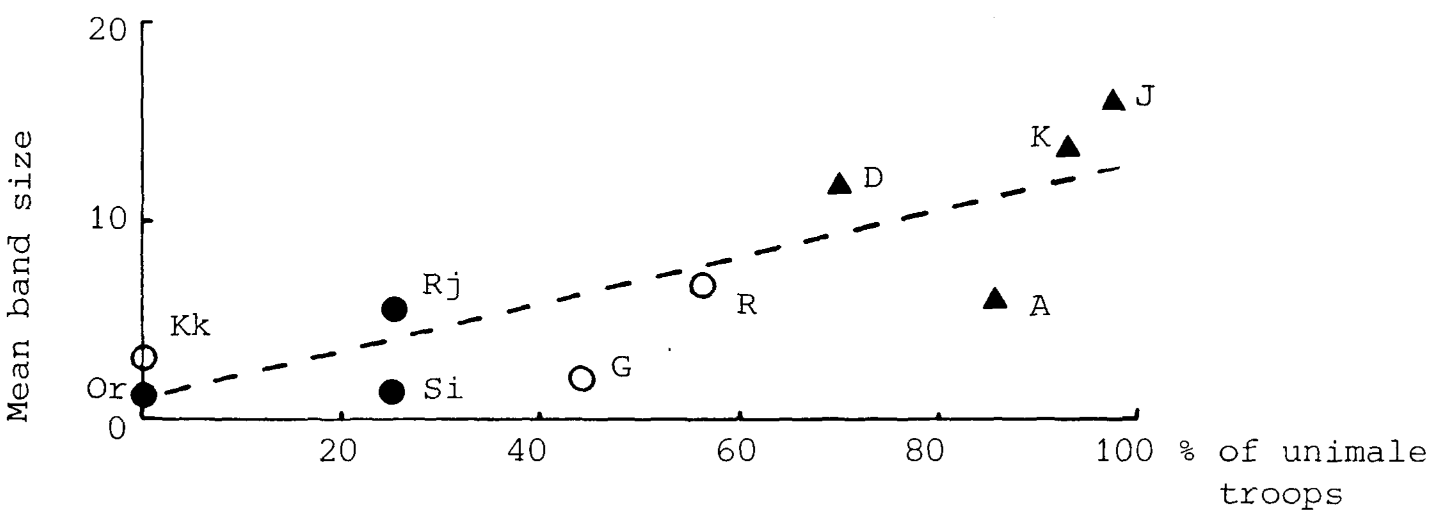


FIG 6.8 RELATIONSHIP BETWEEN % OF UNIMALE TROOPS AND BAND:TROOP RATIO.

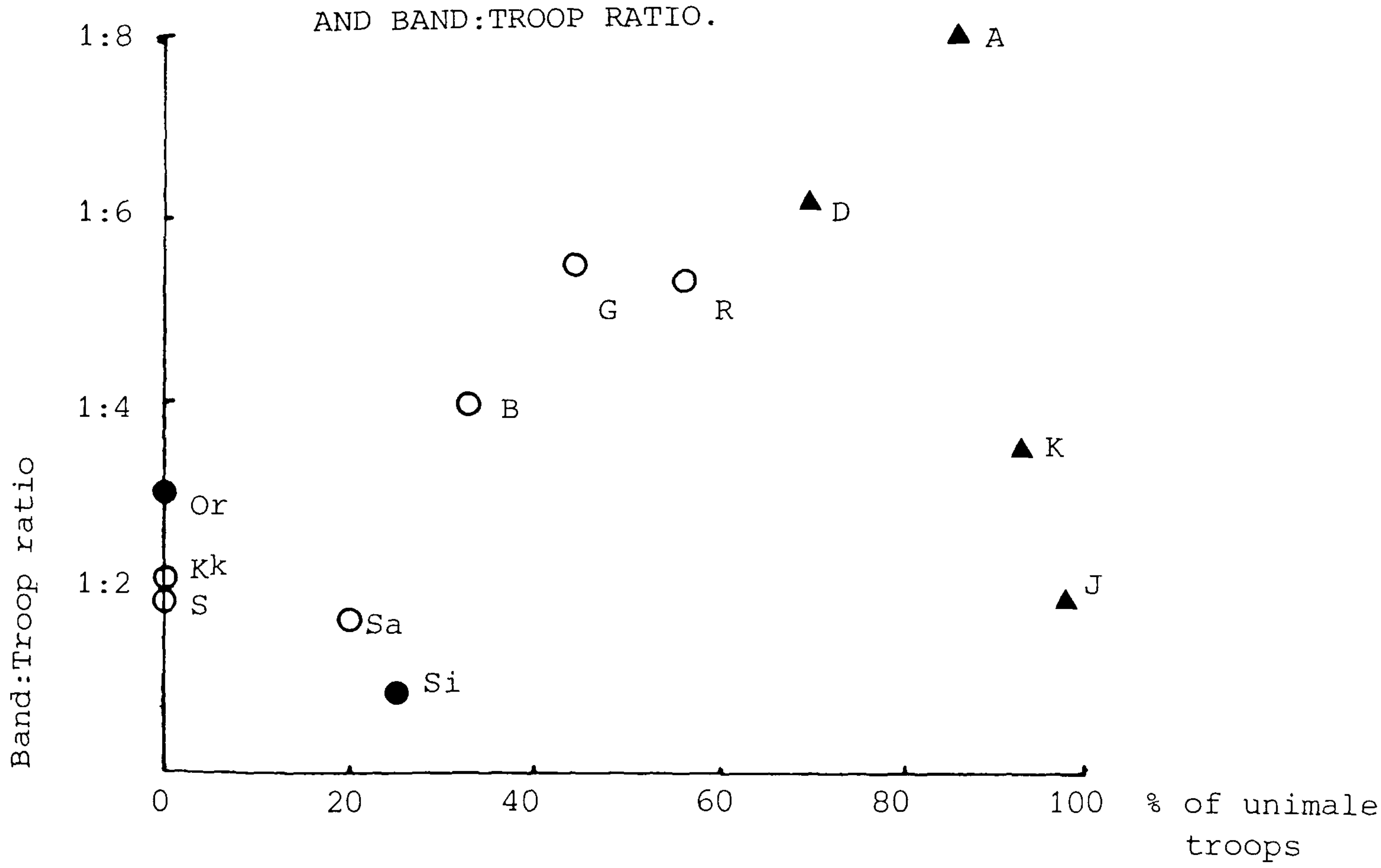


FIG 6.9 RELATIONSHIP BETWEEN LANGUR DENSITY AND % OF UNIMALE TROOPS. (see FIG 6.12 for symbols).

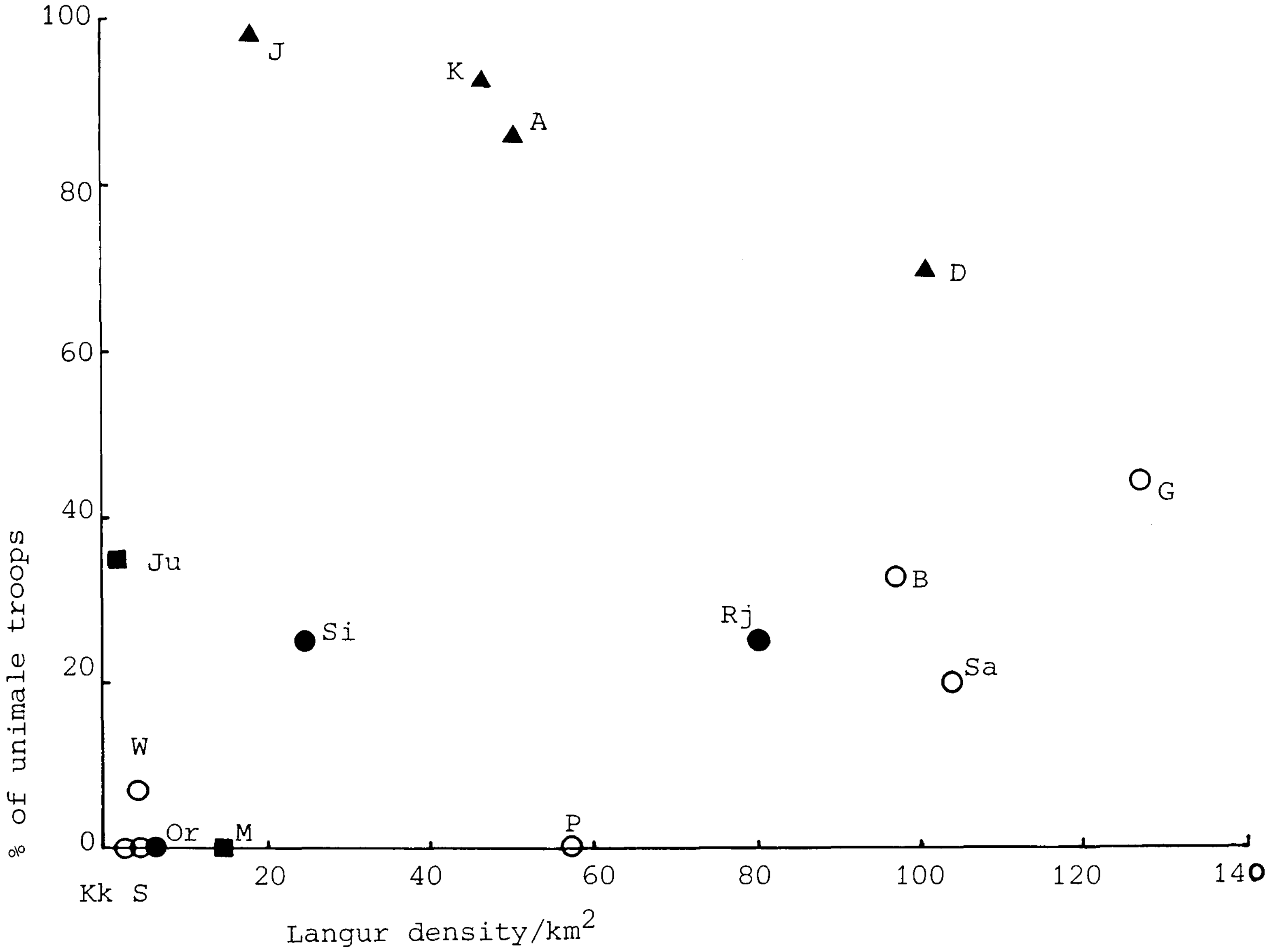


FIG 6.10 RELATIONSHIP BETWEEN LANGUR DENSITY AND % OF EXTRA-TROOP MALES. (see FIG 6.12 for symbols).

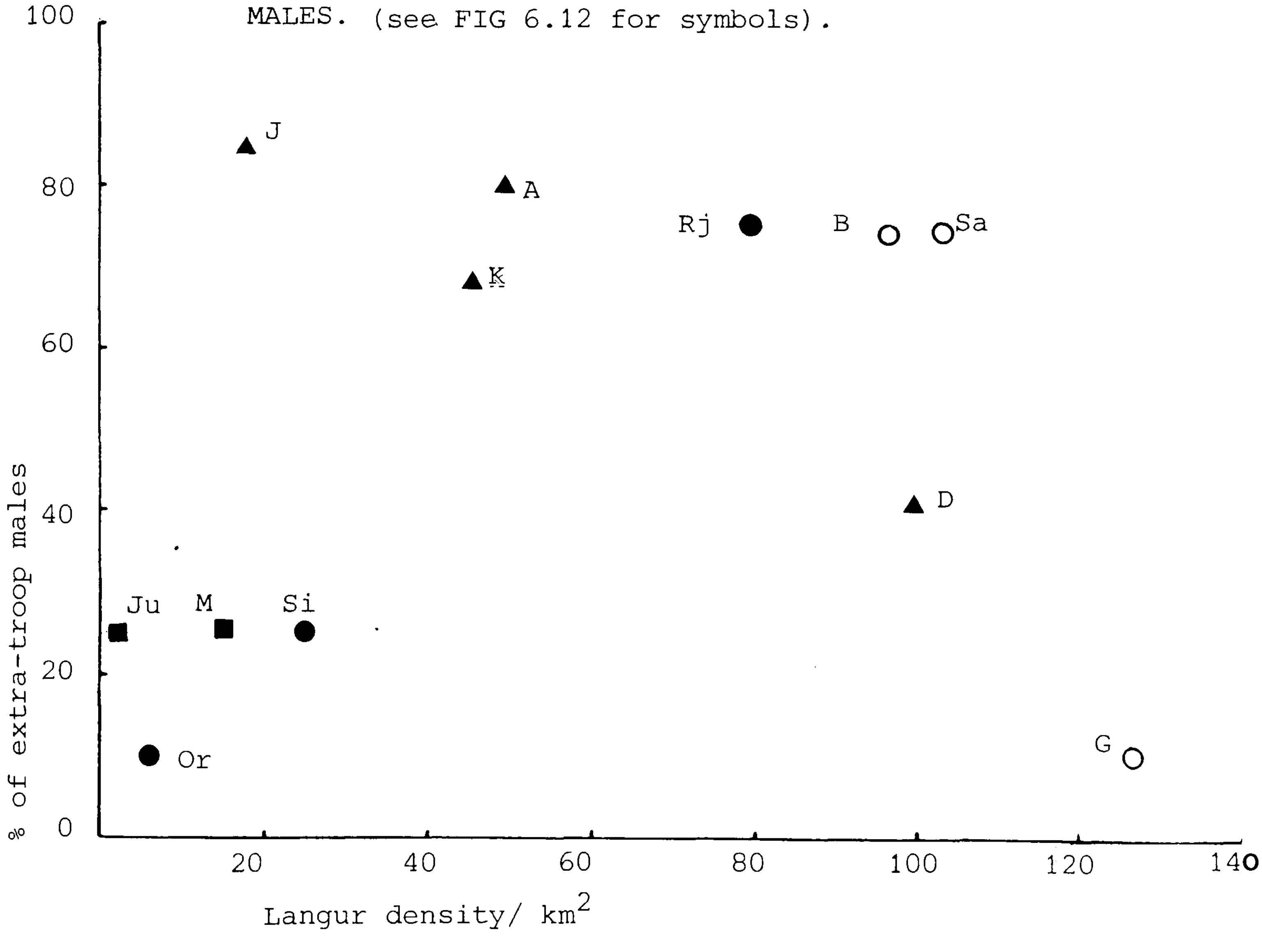


FIG 6.11 RELATIONSHIP BETWEEN LANGUR DENSITY AND TROOP ADULT SEX RATIO. (see FIG 6.12 for symbols).

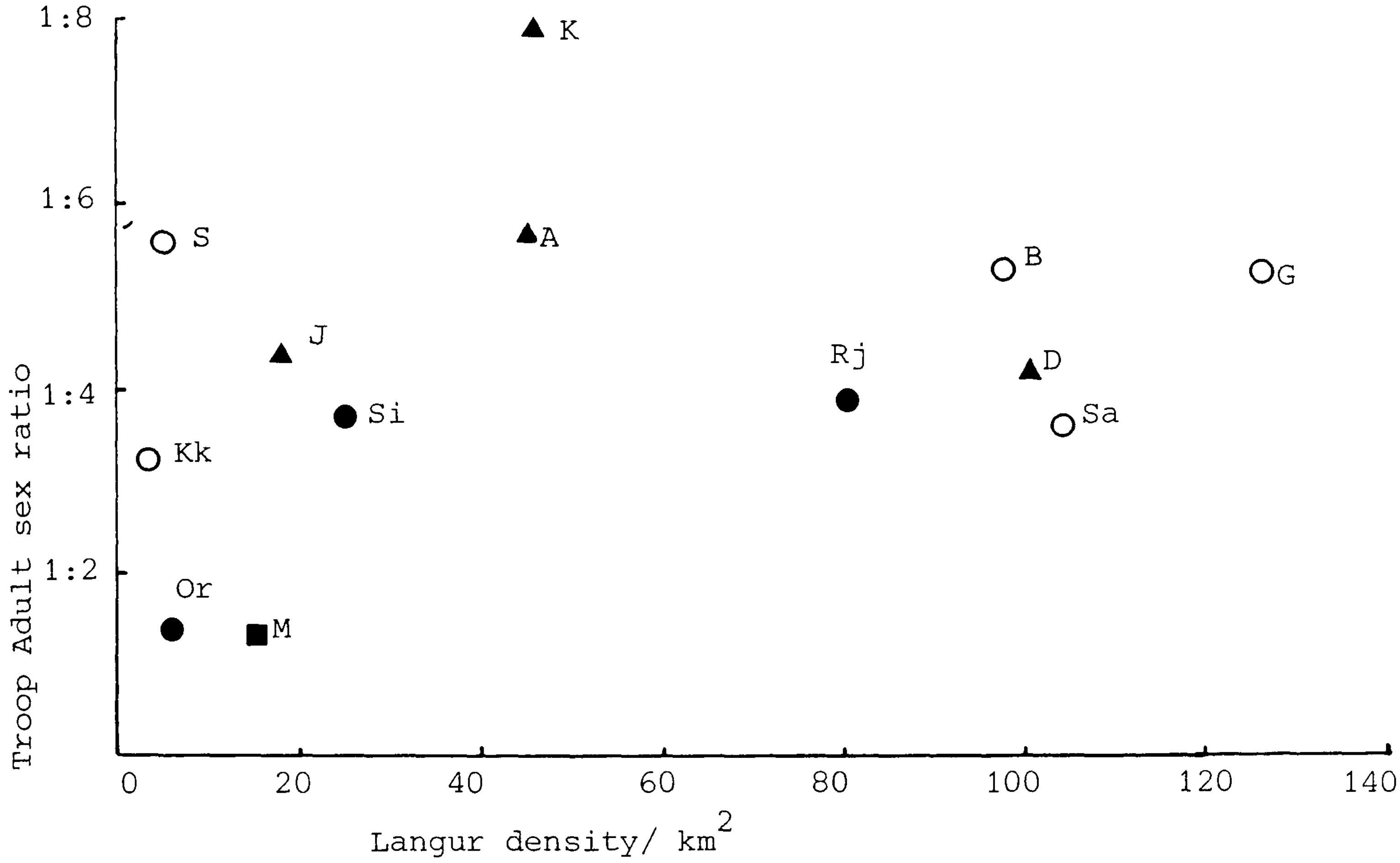
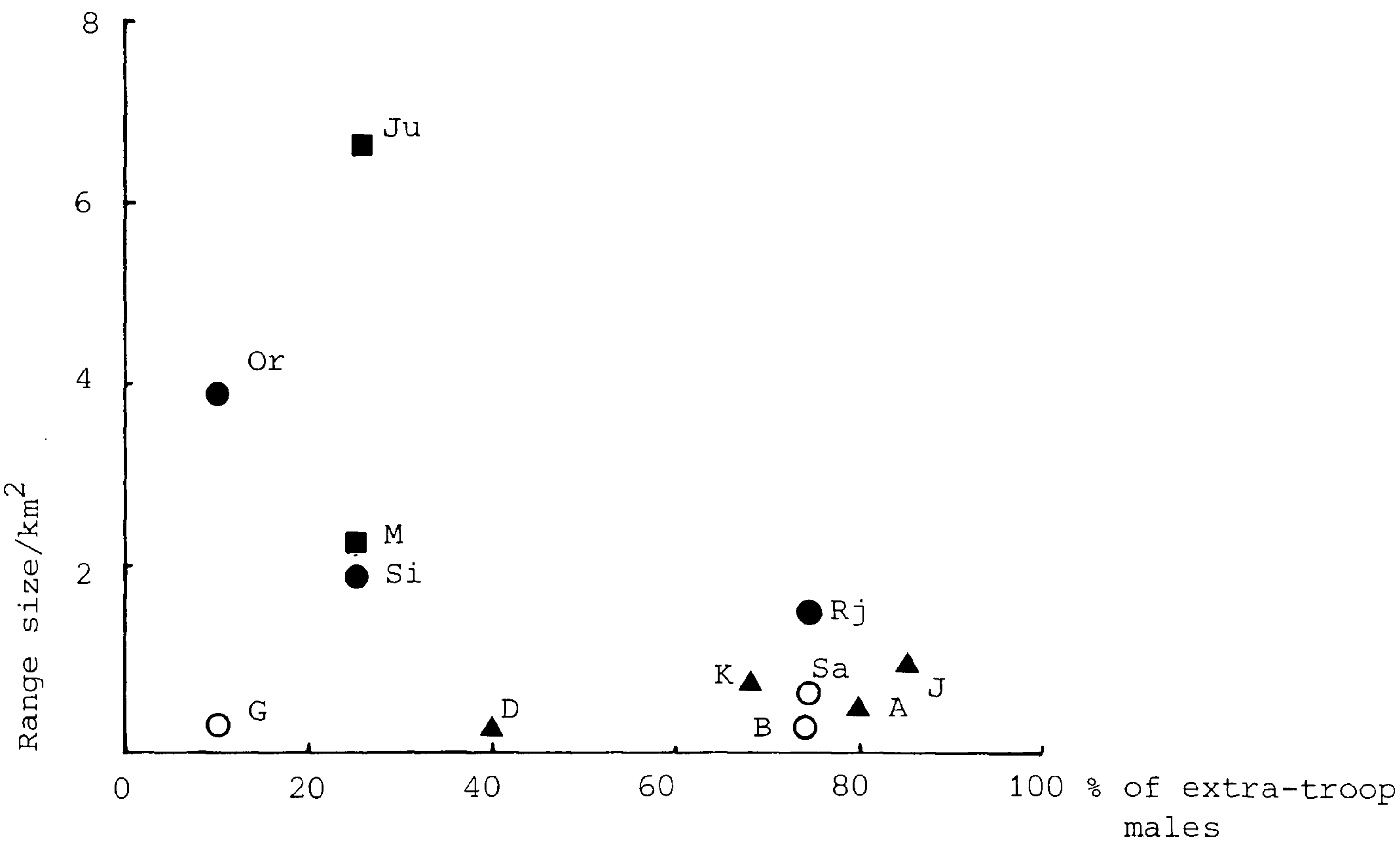


FIG 6.12 RELATIONSHIP BETWEEN % OF EXTRA-TROOP MALES AND RANGE SIZE.



KEY:

○ :Brief studies,small sample sizes.

▲ :Detailed investigations with infanticide & takeover.

■ :Detailed investigations with gradual male replacement.

● :Detailed investigations with equivocal social change.

(See Table 6.C for site abbreviations.)

FIG 6.13 MONTHLY VARIATION IN "C" TROOP SIZE AND CHANGES IN MEMBERSHIP.

(Each ● shows the troop size at the end of the month)

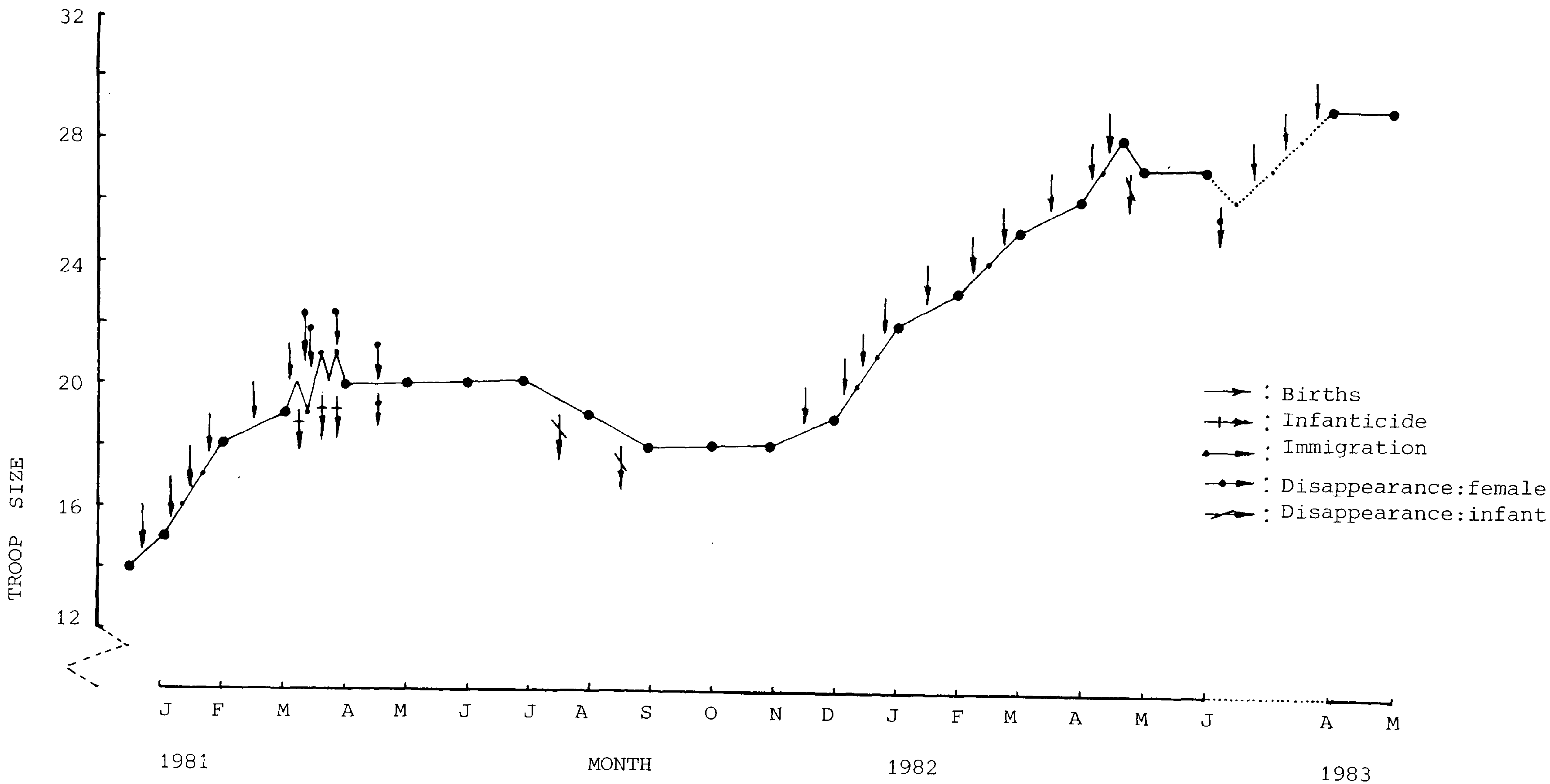


FIG 6.14 MONTHLY VARIATION IN FREQUENCY OF COPULATIONS AND BIRTHS.
"C" TROOP.

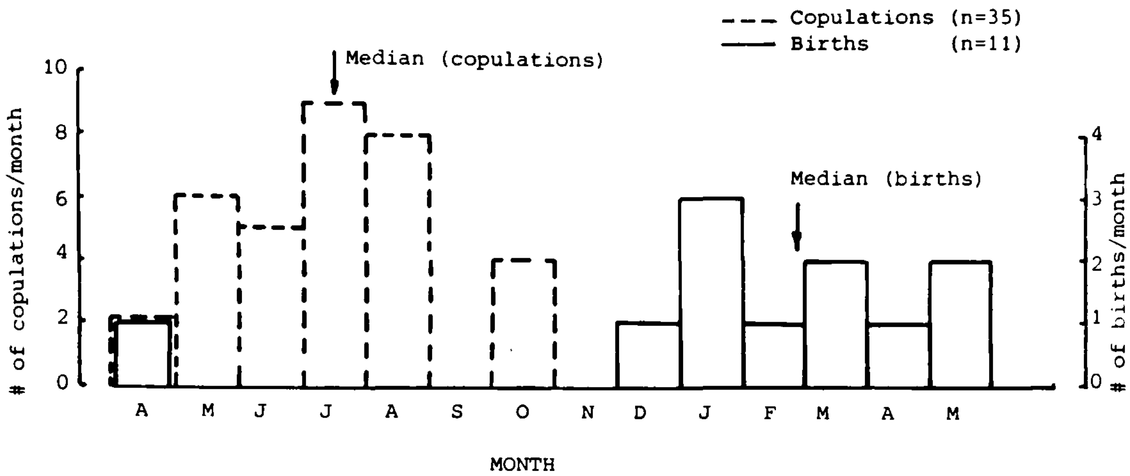


FIG 6.15 MONTHLY VARIATION IN FREQUENCY OF SOLICITS (N=313).
"C" TROOP.

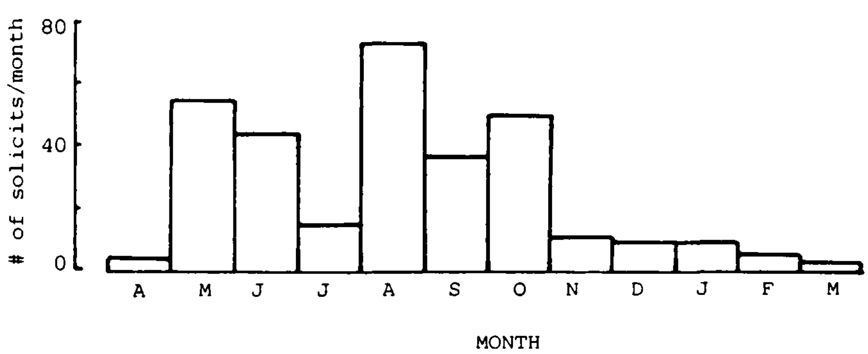


FIG 6.16 MONTHLY VARIATION IN FREQUENCY OF DISAPPEARANCES FROM "C" TROOP.
(N=7).

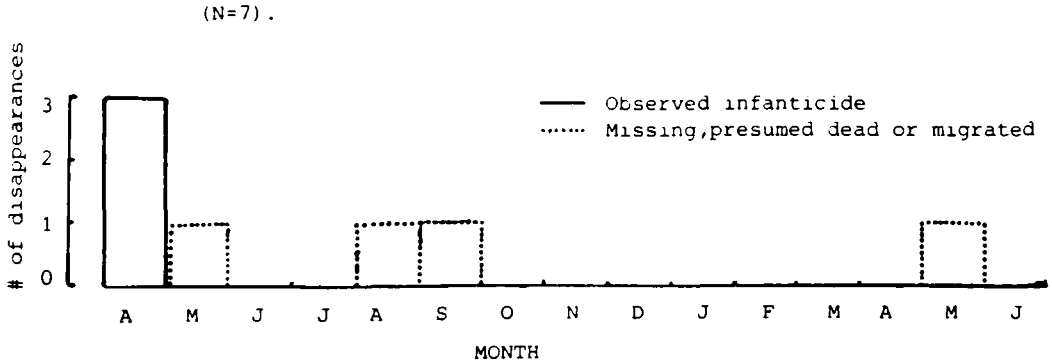


FIG 6.17 HANUMAN LANGUR BIRTH SEASONS AT 13 SOUTH ASIAN STUDY SITES. (Data from Vogel 1977,Bishop 1979, & Laws & Vonder Haar Laws 1984).

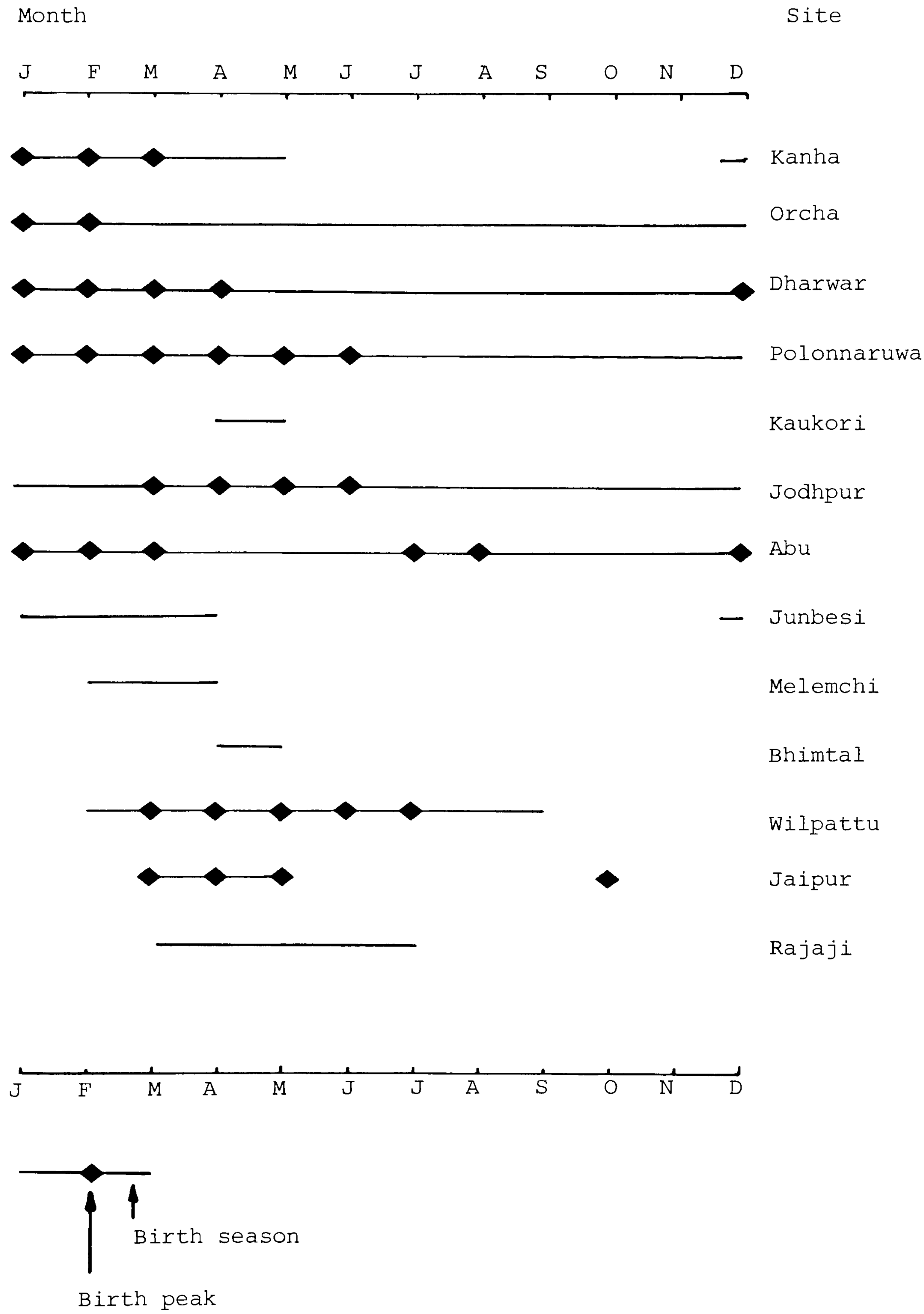


FIG.6.18 CATEGORIES OF INTER-GROUP SOCIAL CHANGE.
Types of langur social change are categorized into the following classes and the simplified essentials of change are illustrated below with examples from the literature. (see text).

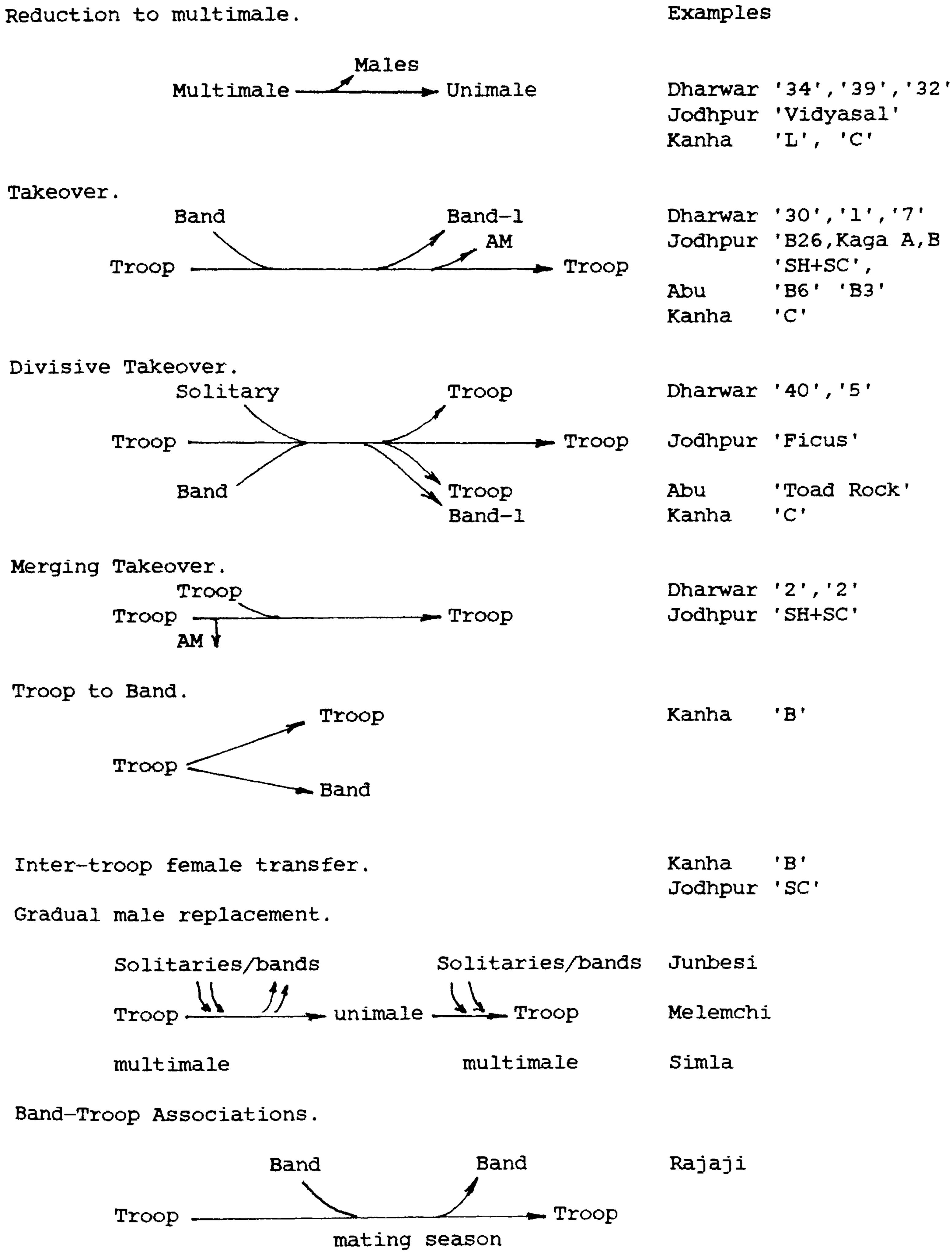


FIG 6.19 DIAGRAMMATIC SUMMARY OF SOCIAL CHANGE IN "L" TROOP.

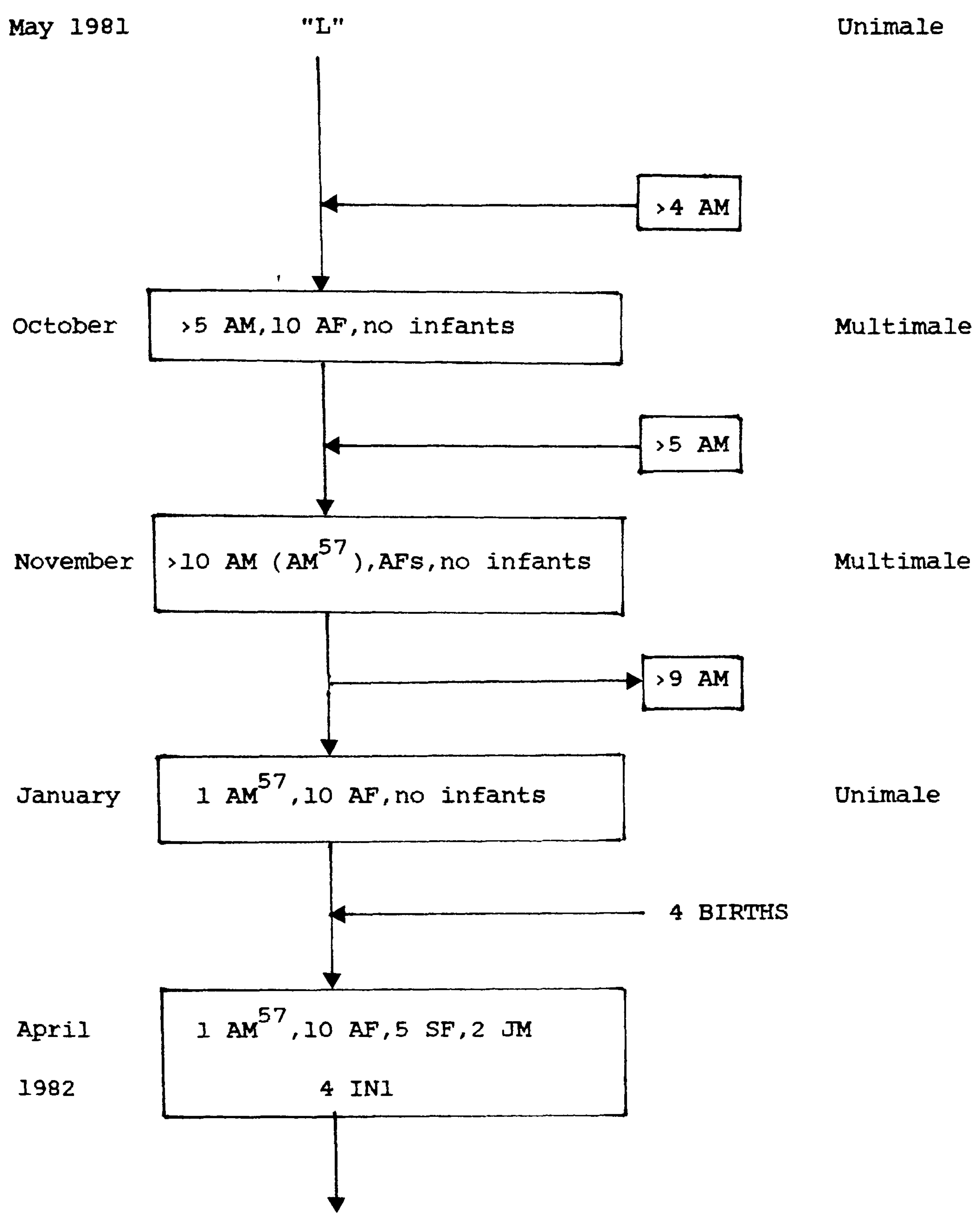


FIG 6.20 DIAGRAMMATIC SUMMARY OF SOCIAL CHANGE BETWEEN "B" AND "C" TROOPS.

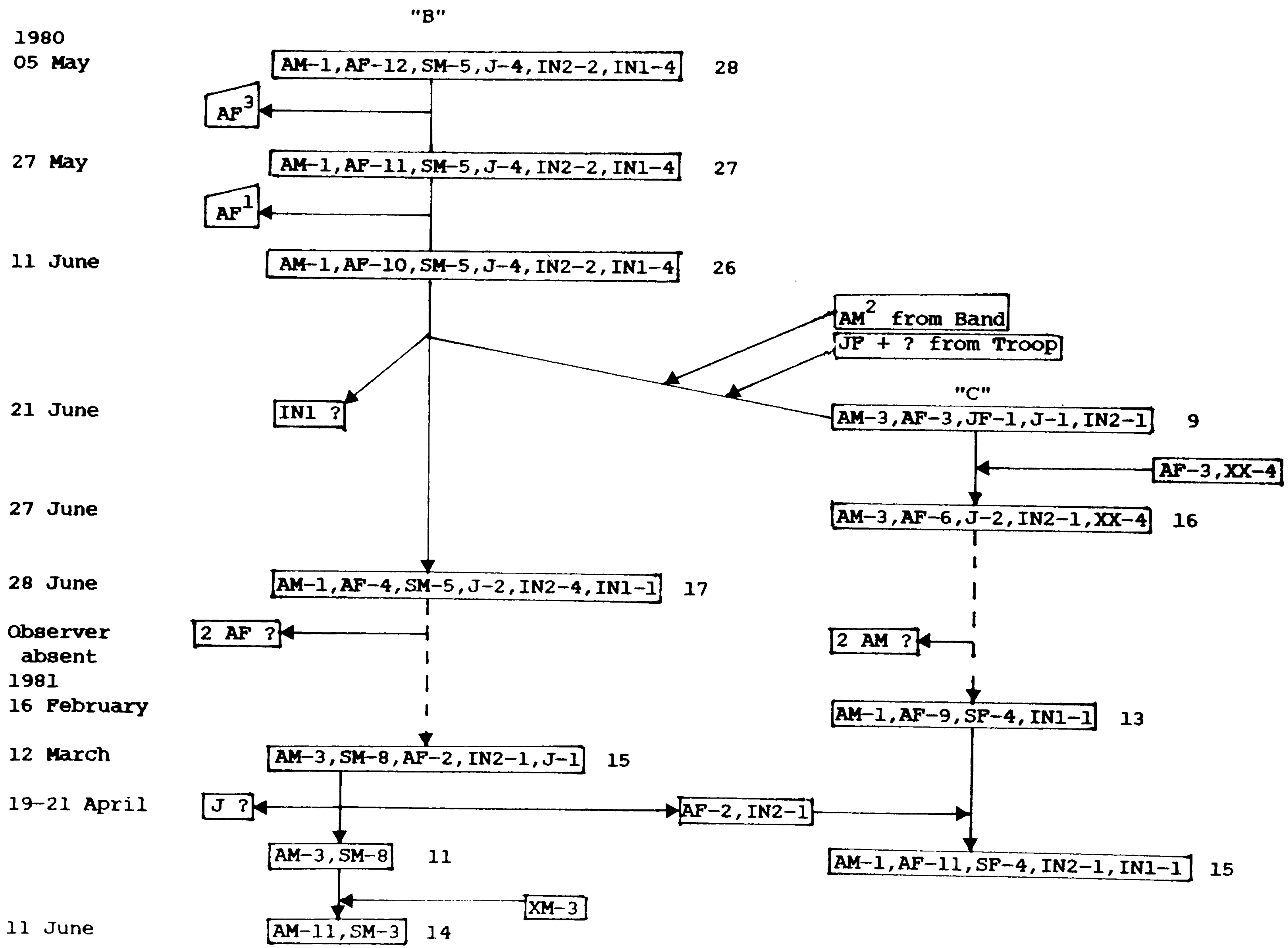
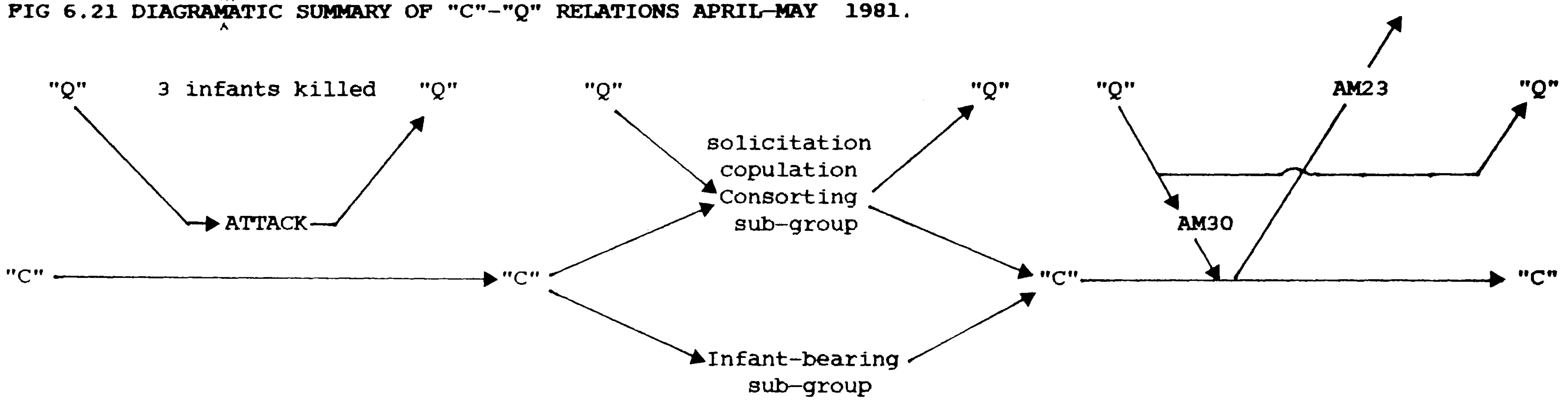
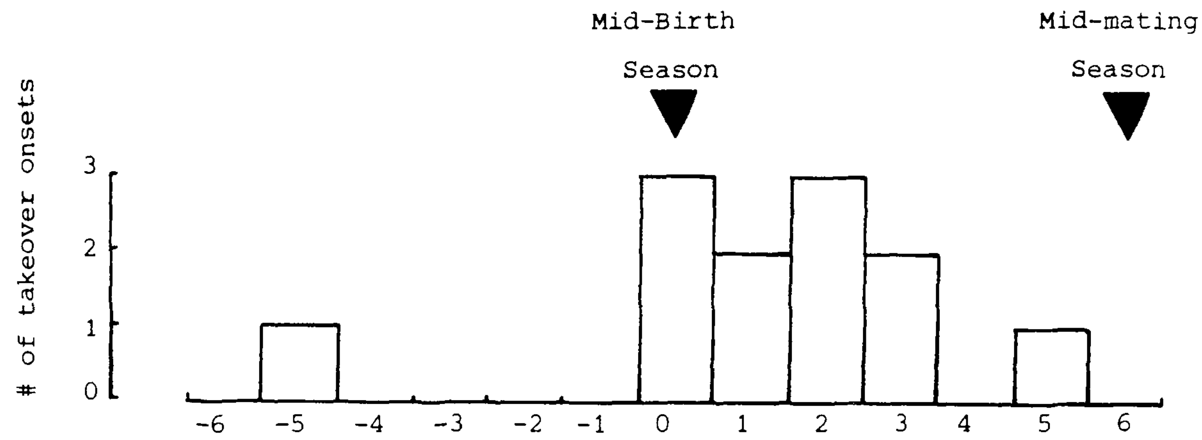


FIG 6.21 DIAGRAMMATIC SUMMARY OF "C"-"Q" RELATIONS APRIL-MAY 1981.



18 April — 21 April	22 April — 4 May	5 May — late June
PHASE 1: INFANTICIDE	PHASE 2 :POLARIZATION AND CONSORTING	PHASE 3:TAKEOVER,ADULT MALE-FEMALE CONFLICT
18 April - 21 April No.days observation:4 full days Mean observation hours/day :13 hours	22 April - 4 May 6 full days + visits on 5 days 8.3 hours	5 May - late June May : 12 full days + visits on 8 days 9 hours
Daily attacks by "Q" on "C",three infants killed by band males."C" polarization,infant bearing females fleeing on "Q" arrival into concealment.Unencumbered females approach "Q".AM23 ineffectual in preventing attacks.	On five days "C" forming two diurnal sub-groups, reuniting at night.AM23 and infant-bearing females remain seperate from "Q".Consorting females solicit and four seen to copulate with "Q".On one day "Q" attack infant-bearing females but AM23 supplants band."Q" not observed on five days.	Replacement of AM23 by AM30 of "Q". AM30 attacks 9 month old infant which is observed with injuries."C" occasionally associate with "Q" but by mid-May relations agonistic.Frequent AM30-adult female interactions;male attacks infant-bearing females and other females intervene.Attacks subside in June. First conceptions in late May.

FIG 6.23 TEMPORAL DISTRIBUTION OF TAKEOVER ONSETS RELATIVE TO BIRTH SEASON MEDIAN. Data from Kanha(this study),Abu(Hrdy 1977b),Jodhpur (Mohnot 1971a) and Dharwar (Sugiyama 1965a).



Deviation of month of takeover onset from month of birth season median / months. (excluding monsoon season at Abu & Jodhpur).

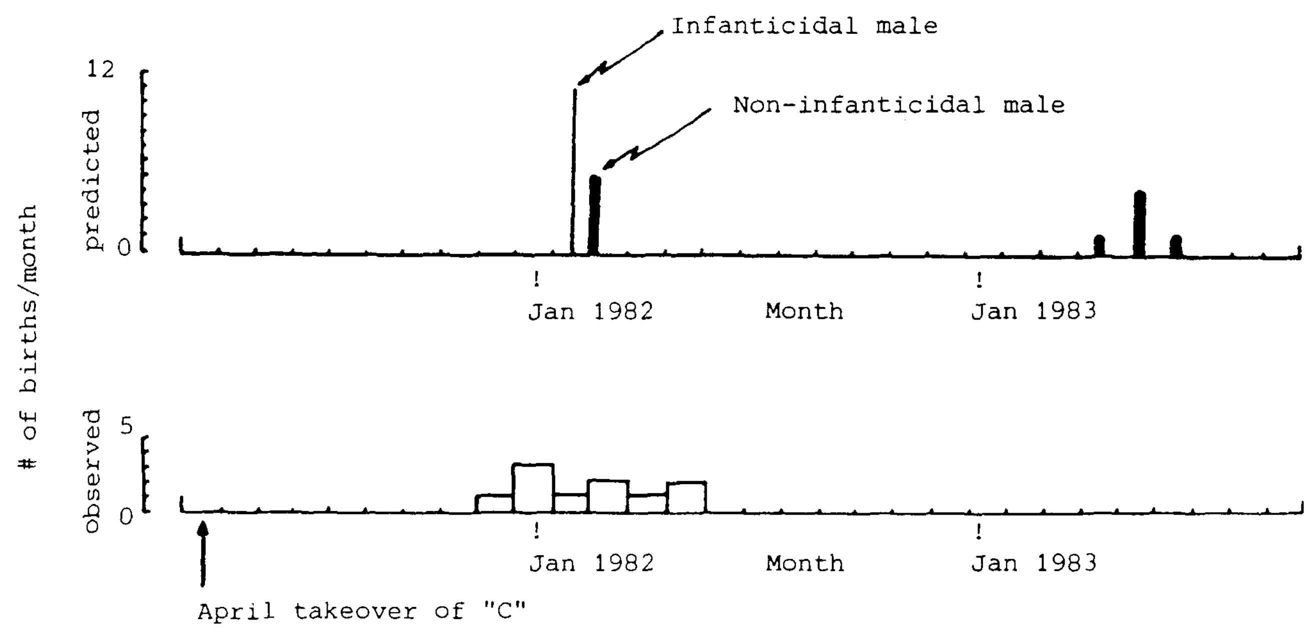


FIG 6.22 COMPARISON OF OBSERVED POST-TAKEOVER BIRTH DISTRIBUTION WITH THAT PREDICTED IF AN INFANTICIDAL (——) MALE OR A NON-INFANTICIDAL MALE (▬) INVADED. (see text for details).

TABLE 6.A:KANHA MEADOW LANGUR POPULATION:SUMMARY.

Population composition-by individuals:

- 360 Langurs
  - 304 in Troops (84.4%)
    - 289 Unimale (95.1%)
    - 15 Multimale (4.9%)
  - 56 in All-Male Bands (15.6%)

Population composition-by groups:

- 18 groups
  - 14 Troops (77.8%)
    - 13 Unimale (92.9%)
    - 1 Multimale (7.1%)
  - 4 All-male bands (22.2%)

	Mean group size	Langur Density	Troop Density	Biomass
	(range)	/km^2	/km^2	kg/km^2
Bisexual troops	21.71(11-34)	38.97	1.79	289.94
All-Male Bands	14.00(8-18)	7.18	0.51	96.03
All groups	20.00(8-34)	46.15	2.31	385.96

Adult sex ratio: All groups 51:127 = 1:2.5
(AM:AF) Troops 16:127 = 1:7.9 (range 1:12 to 1:1.3)

Post juvenile sex ratio : All groups 100:173 = 1:1.7
(juvenile,subadult & adult) Troops 44:173 = 1:3.9

TABLE 6.B DEOTALAO LANGUR POPULATION:SUMMARY.

Population composition-by individuals:

125 langurs → 91 in Unimale troops (72.8%)
→ 34 in All-male bands (27.2%)

Population composition-by groups:

6 groups → 4 Unimale troops (66.6%)
→ 2 All-male bands (33.3%)

Mean group size: (with range)	Troops	22.75 (12-27)
	All-male bands	17.00 (16-18)
	All groups	20.83 (12-27)
Adult sex ratio :	Troops	4:42 = 1:10.50
	All groups	25:42 = 1: 1.68

Biomass and density estimates not calculated owing to ignorance of area sampled.

TABLE.6.C SUMMARY OF HANUMAN LANGUR POPULATION STATISTICS:MAJOR STUDY SITES.

Study site & Abbreviation		Density /sq.km.	Troop size	Band size	Range size/sq.km	%Unimale Troops	Sex ratio Troop	%AM extratroop	Band:troop ratio	Habitat
Kanha *	K	46.15	21.7	14	0.75	93.0	1: 7.9	68.6	1: 3.5	Moist
Orcha *	O	6.2	22	1	3.9	0	1: 1.4	10	1: 3.0	Moist
Rajaji *	Rj	80	46.3	5.5	1.5	25.0	1: 4.0	75	------	Moist
Dharwar *	D	100	14	11.8	0.17	70.4	1: 4.2	40	1: 6.3	Dry
Gir Forest	G	127	30	2	0.3	44	1: 5.3	10	1: 5.5	Dry
Polonnaruwa	P	58	25	—	0.12	0	------	—	------	Dry
Wilpattu	W	4.2	23.8	—	—	7	------	—	------	Dry
Sariska	Sa	104	64	—	0.6	20	1: 3.6	74	1: 1.7	Thorn
Kaukori	Kk	2.7	54	3	7.8	0	1: 3.2	—	1: 2.0	Village
Jodhpur *	J	18.1	35	15.7	0.95	98	1: 4.3	85	1: 1.8	Village
Abu *	A	50	21	6	0.38	86	1: 5.7	80	1: 8.0	Village
Singur	S	4.6	13	—	0.43	0	1: 5.6	—	1: 2.0	Village
Raipur	R	—	29.1	6.9	—	56.3	1: 5.7	29	1: 5.3	Village
Junbesi *	Ju	2	11	—	6.6	35	------	25	------	Himalayan
Melemchi *	M	15.2	32	—	2.17	0	1: 1.3	25	------	Himalayan
Simla *	Si	24.6	48	1.8	1.90	25	1: 3.7	25	1: 0.9	Himalayan
Bhimtal	B	97	23	—	0.2	33	1: 5.3	74	1: 4.0	Himalayan

See 6.3.3 for explanations of variables. Source: Hrdy (1977b), Vogel (1977), Oppenheimer (1977), Bishop (1979) Boggess (1980), Laws & Vonder Haar Laws (1984) & this study.

*: site allotted to 'detailed' subset / Habitat: Moist=Moist deciduous forest; Dry=Dry deciduous forest; Thorn=Thorn forest; Village=Village & Cultivation; Himalayan=Himalayan Forest.

TABLE 6.D LIST OF OBSERVED LANGUR TAKEOVERS AND INFANTICIDE.

* = initiated by experimental removal of adult male / No. Infants killed : x = killing seen by author
Month = month of takeover initiation (x) = wounding seen by author
T = Takeover, DT = Divisive takeover, MT = Merging takeover. [x] = killing or wounding seen by informant.
Males after : 1/1= two resulting troops,one male in each; 1,1 partial takeover by two males.

Troop		Month	No of Infants Prior	Missing	Killed	AM-AFIN1 Attacks	No of Adult Males Before	After	Source	Takeover Type	Source
Dharwar	30	May	5	5	(1)	/	1	1	Band	T	Sugiyama (1965a)
	1	March	4–5	4–5	–	x	3	2	Band	T	Sugiyama (1967)
	7	Oct	6	0	0	/	1	1	Band	T	Sugiyama (1967)
Jodhpur	B26	July	4	4	2 (3)	/	0	1	Band	T	Mohnot (1971a)
	Kaga B	April	19	3	–	/	1	1	Band	T	Makwana (1979)
	Kaga A	April	20	0	0	/	1	1	Band	T	Makwana (1979)
	SH+SC	June	9	0	0	x	1	1	Band	T	Makwana & Advani (1981)
Abu	B6	July	6	6	[2]	x	1	1	?	T	Hrdy (1977b)
	B3	March	3	3	[2]	x	3	1	Troop	T	Hrdy (1977b)
	B6	June	4	3	[1],(1)	/	1	1,1	?	T partial	Hrdy (1977b)
	B6	Feb.	1	1	(1)	/	1,1	1	Band	T	Hrdy (1977b)
	B3	?	?	?	?	?	1	1	Troop	T	Hrdy (1977b)
	B6	?	?	?	?	?	1	1	Band	T	Hrdy (1977b)
	B3	April	?	?	[1]	/	1	1	Troop	T	Hrdy (1977b)
	B6	?	?	?	?	?	1	1	?	T	Hrdy (1977b)
Kanha	C	April	6	6	2 (3)	/	1	1	Band	T	this study
Dharwar	40	Aug.	2	0	0	?	1	1/1	?	DT	Sugiyama (1967)
	5	July	?	0	0	?	1	1/1	Band	DT	Sugiyama (1967)
Jodhpur	Ficus	April	?	?	?	?	1	1/1	Band	DT	Makwana & Advani (1981)
Abu	Toad	?	?	?	?	/	1	1/1	?	DT	Hrdy (1977b)
Kanha	C	June	?	?	?	x	0	3	Band	DT	this study
Dharwar	2 *	June	4	4	0	/	0	0	Troop	MT fail	Sugiyama (1966)
Dharwar	2 *	Oct.	0	–	–	–		1	Troop	MT	Sugiyama (1967)
Jodhpur	SHSC	March	8,4	0	0	?		1	Troop	MT	Makwana & Advani (1981)

CHAPTER 7

ACTIVITY PATTERNS

CHAPTER 7 ACTIVITY PATTERNS.

7.1 INTRODUCTION

This chapter describes the proportion of time langurs of "C" troop spent in different activities and its variability between months and age/sex classes. The annual activity budget of langurs has not been previously documented in undisturbed forest. Inter-relationships between activity patterns and feeding ecology are considered in Chapter 10. As this chapter is the first to use systematically collected langur scan data the methods, outlined in Chapter 3, are described, the reasons for their choice given and potential bias considered.

At night langurs roost in trees and are inactive apart from occasional shifts in position or disturbance by nocturnal predators (Roonwal & Mohnot 1977, pers.obs.). Therefore no systematic observations were made at night and all results presented here refer to proportions of daylength.

7.2 METHODS.

A major objective of this study was to investigate the proportion of time langurs spent in different activities, fed on different items and occupied diverse parts of their range. A sampling regime was therefore required which estimated the proportion of time langurs spent in different 'states' (Altmann 1974), for example, feeding on Shorea fruits, playing, or occupying a certain quadrat. The acquisition of this type of data was of higher priority than the recording of 'events' such as copulations or transitions between quadrats (Altmann 1974). Altmann's (1974) 'observer's guide' suggested two techniques which were potentially appropriate; scan sampling and focal animal sampling.

In scan sampling the observer records the behaviour of all visible animals at a particular time, producing an estimate of the proportion of the troop engaged in the states being investigated. When scans are repeated frequently, by scheduling at regular intervals, an estimate can be obtained of the proportion of total time the entire troop and the constituent age/sex classes spend in each recorded state. Scanning has the advantages that it is relatively easy to sustain in the field, individual animals need not be identified and followed, and it yields large amounts of data. Scanning does however potentially suffer from bias caused by :

a/differential visibility of different activities

b/differential representation of age/sex classes.

c/differential visibility at different times of day.

The second method, focal animal sampling, as used by Yoshiba (1967), Richard (1977), requires an animal to be chosen, preferably at random, and followed for a sample period. The activities of that animal are recorded continuously, with the observer determining onset and end of observation bouts independently of the subject's activity, producing information on duration and sequencing of 'states' and also of 'events' (see Altmann 1974, Clutton-Brock 1977c). Focal animal sampling has the advantage that the above biases are less likely to be important than data collected during scans. The technique does, however, suffer from the following disadvantages :

a/the target animals must be well habituated to the observer to tolerate long periods of being followed.

b/it is not practicable to follow individuals for long periods in forests due to problems of visibility and access to the animal.

c/in comparison to scans a relatively small amount of data can be collected per unit time (Clutton-Brock 1977c) and it is also more difficult to sustain accurate recording for long periods.

Focal animal sampling was attempted at the beginning of the study. Although the langurs were sufficiently habituated, the observation conditions were too difficult, due to obscuring vegetation, for it to be practical. Focal animal sampling of langurs 30m up a densely foliated tree was found to be impossible. Therefore, although focal animal was theoretically superior in data quality, pragmatics necessitated scan sampling for all systematically collected langur data on activity, ranging and feeding. The visibility biases noted above are discussed in more detail in 7.3.1.

Three methods have been suggested for the time scheduling of scan samples, 'instantaneous', 'duration' and 'delayed'. An instantaneous scan is recorded if each animal's state is recorded instantly at a pre-arranged time. However, in practice such speed of observation and recording is not possible and at best it consists of recording each individual's state at the moment the observer first saw it during the scan (Altmann 1974, Clutton-Brock 1977c). As Altmann (1974) notes, each individual should be scanned for the same brief period of time or the sample would become equivalent to a series of short focal animal samples of variable and unknown duration. This bias can be reduced by using few, and easy to score, categories.

This extensively used method of scanning (e.g. Clutton-Brock 1972) has been challenged by Struhsaker (1975) who suggested the alternative of 'duration' scanning. Struhsaker (1975), Oates (1977a), Waser (1977a) recorded the first activity to last uninterrupted for > 5 seconds for each animal observed per scan. In principle this would allow a more accurate classification of categories hard to achieve in instantaneous, 'at a glance' recording. However, as a consequence of the time delay it tends to select against activity bouts of about 5 seconds and totally excludes activities lasting less than 5s (Clutton-Brock 1977c). Struhsaker (1975,p177) considers this as an additional advantage of the technique, claiming that one should "distinguish a brief pause between mouthfuls during a feeding bout from a 20 minute siesta." He suggests that to classify these two 'types' of inactivity in the "same category constitutes a serious misrepresentation of the . . . time budget". However, as Clutton-Brock (1977c) notes there appears to be no evidence that inactivity during feeding is essentially different from longer periods of inactivity. If, for example, there were a discontinuity in the frequency distribution of bout lengths the discrimination might be justified. Also, without such evidence, the choice of a 5s duration is arbitary and will bedevil interspecific comparisons should species be variable in the distribution of bout lengths.

The use of 'delayed' sampling, in which the animal's 'state' is recorded at a fixed time interval after it was first seeen (Clutton-Brock 1977c) probably avoids the problems of the observer trying to do many things simultaneously as in 'instantaneous' sampling and the confounding problems of 'duration' sampling. In practice, however, it may be confusing to use with a large number of animals and will be more time consuming.

The importance of the differences between instantaneous and duration scanning are illustrated by comparisons of Struhsaker's (1975) and Clutton-Brock's (1972) investigations of two different red colobus (C.badius) troops in the Kibale forest in Uganda. The former using duration sampling scored inactivity 20-26 % less often and feeding 16-20 % more often than Clutton-Brock using instantaneous scans. Such large differences within the same population are more likely to be an artefact of methodology than biological variation (Struhsaker 1975). Marsh (1981a) also working with red colobus, used both techniques concurrently and found small but significant differences between the two budgets mainly in feeding and moving. Oates (1977a), for black and white colobus (C.guereza) recorded, for four days, duration sampling with 5s and 2s interval lengths, the latter approximating to instantaneous scanning. Marked differences were found for moving, which was twice as frequent in instantaneous than in duration recording.

Therefore these two different sampling methods can produce important differences, quite unrelated to monkey ecology, and the lack of standardization casts doubt on the validity of interstudy comparisons. In this project instantaneous sampling has been used throughout, despite the problem of retrospective judgements when attempting to record 14 langurs 'at an instant'. Duration sampling was not used because of the arbitrary nature of the time interval and the lack of justification for discriminating between long and short bouts of inactivity. Delayed scanning was not used because of the extra time required and increased potential for confusion. However, in retrospect I feel that the latter method would have provided a useful comparison with instantaneous sampling and should have been used as a check. Ideally, focal animal sampling would be used as a comparison but this check was negated by the observation conditions. At a study site where visibility is less of a problem it might be illuminating to attempt both concurrently.

Scan samples were scheduled every half-hour between dawn and dusk. Initially, quarter-hour samples were attempted but with some fourteen langurs recorded per scan it was not found possible to maintain the regime. On the very rare occurrences that a scan was missed on the half hour the scan was postponed 5 minutes.

For each scan I positioned myself strategically to gain the best view of the troop, without causing disturbance, and recorded nine variables for each visible langur. A fictional example of the type of checksheet used is given in Fig 7.1. The area encompassing the troop was then searched for any further animals which were sampled up to 10 minutes from the onset of the scan. However > 80 % of langurs were recorded within the first five minutes. The observations recorded for each individual langur within scans are termed 'records', of which there were a mean of 14.4 per scan (therefore about 71 % of "C" troop was sampled per scan).

The onset and end of daily scans was independent of langur activity and dependent on the time of sunrise and sunset (Fig 3.2). The time of the first scan varied from 05.30 to 07.00 and of the last from 17.00 to 18.30 (Fig 7.2). The categories of activities recorded were defined (after Clutton-Brock 1972, Marsh 1978) as follows;

INACTIVE :stationary, without moving limbs, including sleeping, resting and staring around.

MOVING :locomotion of the whole body. Sometimes difficult to distinguish from playing. Moving was subdivided into moving within trees, between trees and on the ground. These three subcategories are lumped in the analysis, except where mentioned in the text.

FEEDING :Inspection, manipulating, chewing or ingesting a potential food item.

SELF-GROOM :One animal scratching, examining or removing items from own fur.

ALLO-GROOM :Grooming or being groomed by a conspecific.

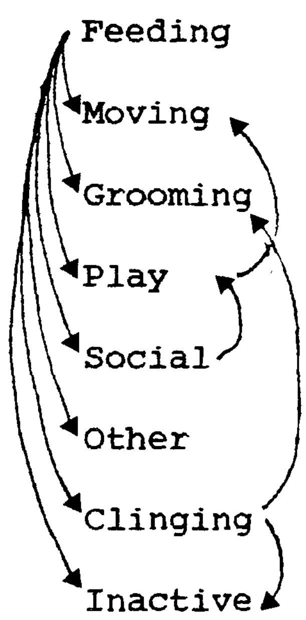
PLAY :Chasing, wrestling, gambolling behaviour by immatures, including solitary play.

SOCIAL :Social interactions between two or more langurs, excluding play and allogrooming.

CLINGING :Clutching of ventral surface of females by immatures.

OTHER :Activities not falling into the above categories, including drinking and interspecific interactions.

Space on the right hand side of the checksheet (Fig 7.1) was left for ad-lib notes and elaboration on the scan scores. For example 'social' and 'other' entries would be detailed and food items described. Occasionally, an animal was engaged in two activities concurrently, in which case one activity was given priority according to the following scheme, similar to that used by Marsh (1978) :



X ⟶ Y indicates that activity X was given precedence over activity Y. The decision of allotting priority reflected interest in feeding, but rarely had to be invoked.

The SCAN checksheet data were typed into the filestore of the ICL 2988 Computer at the University of Oxford Computer Service and analysed using SPSS (Nie et al 1975) and MINITAB (Ryan et al 1981), on the VAX computer.

The activity data, presented here, are derived from the five SCAN 'follows' per month. The contribution of each activity category to the monthly budget was expressed as the number of records per activity as a percentage of the total number of records in each month. The annual budget was calculated as the mean of the twelve monthly budgets.

7.3 ACTIVITY PATTERNS : RESULTS.

7.3.1 ANNUAL BUDGET AND BIAS.

The annual budget for "C" troop is shown in Table 7.A and in Figs 7.3,7.4. Over the twelve month cycle the troop spent 41.8% of daylight hours inactive and 25.7% feeding which, together with 13.1% moving, 7.9% clinging and 6.0% allogroooming, constituted 91.7% of daylight hours. The remaining time was spent in selfgrooming, play, social and 'other' behaviours. In 1.9% of records the activity category was unrecorded. Before seasonal and age/sex class variations are considered the biases to which scan data is liable, alluded to in 7.2, will be discussed.

A/ Differential visibility between activity categories.

If the majority of "C" were visible when the predominant troop activity was, for example, moving and a minority visible when most were, say feeding, the scan sampling would overestimate the proportion of time spent moving. Such association between predominant activity and the number of records per scan can be tested for by treating the data collected in each scan equally (Clutton-Brock 1972,1974b). This equalization was carried out on a subset of the data, the months of May, August and December (i.e one month from each season). The number of records per activity in each scan were expressed as the percentage of the total number of records made in each scan (Clutton-Brock 1974b). For each day 'follow' medians of the resulting percentages were calculated and medians of these medians tallied for the five days of 'follows' per month. Because of the high frequency of zero values for many activities and marked skewness of the distribution truncated medians (B.Don pers.comm.) were used. This alternative analysis (Method B) resulted in three monthly activity budgets, in which each scan has equal weight, which can be compared with the original technique (Method A) of weighting scans according to the number of records within them. The results produced by the two methods are highly correlated (Fig 7.5; May:r_s=0.997,n=12,p<0.001, August:r_s=0.998,n=12,p<0.001, December:r_s=0.998,n=10,p<0.001). This suggests that at least for the three subsampled months, bias resulting from association between predominant activity and number of visible langurs per scan was, if present, not an important influence.

However, as noted by Clutton-Brock (1974b) bias could still be introduced by differences in the probability of detecting activities owing to visibility differences. Without focal animal sampling, recorded concurrently with scan sampling, this bias cannot be adequately tested for. It would be expected to result in overestimation of the importance of moving and inactivity and underestimation of feeding. As discussed in 7.3.2 the seasonal pattern of feeding time shows the opposite pattern to that expected if visibility bias was a determining factor.

B/ Differential representation of sex/age classes.

The troop activity budget is an aggregate of the behaviour of each "C" animal. Individuals would be expected to show variability in how they allocate their time. The largest differences would be predicted between, rather than within, the age/sex classes (as defined in Table 4.A) due to variation in body size and physiological factors such as lactation, pregnancy and maturation. If these classes are not represented in the scan data in the same proportion as they are found in the troop, the budget would not be representative of group activity. In addition, if the troop composition changed during the year the budget may change thus confounding seasonal variation (Marsh 1981a).

As depicted in Fig 7.4 and further discussed in 7.3.2. there are differences between langur age/sex class activity budgets with infant budgets particularly disparate. Therefore if, for example, infant-ones were over-represented in the scan data there would be a tendency for the aggregate budget to be biased towards clinging.

The percentage frequency of the occurrence of each langur class in scans is compared with that expected on the basis of mean troop composition in Fig 7.6 for twelve months of lumped data. The expected and observed are very similar with adult males, females, juvenile females and infant-twos being slightly over-represented and subadult-females and infant-ones being slightly under-represented in the observed. The largest discrepancy is for the infant-one class with a deviation of -2.3%. Statistical tests for examining the significance of these deviations were not used as they are violated by a lack of independence; the same animals were frequently recorded in successive scans, inflating the sample size and presumably increasing the probability of a Type II error (Siegel 1956,Clutton-Brock 1974). Clutton-Brock (1974b) and Oates (1977a) found similar agreement between expected and observed and concluded that there was no evidence of gross bias due to differential representation of age/sex classes. However Fig 7.7 reveals that the lumped data conceal considerable intermonthly departures of expected from observed scan composition. The adult male and to a lesser extent the infant-twos are consistently over-represented. The monthly analysis also reveals considerable, but inconsistent, differences for other classes. Adult and sub-adult females deviations tend to be inversely related. The largest departures from expected occurred during March when adult females were over-represented by 6.3% and infant-ones under-represented by 8.6%. Therefore, although annual departures may be small there are considerable discrepances, hidden by inconsistency, which may confound intermonthly comparisons.

The maximum effect of this bias on the annual budget can be assessed using the method of Marsh (1981a) whereby a corrected estimate is calculated for an activity largely restricted to one or two classes. Here clinging, mostly exhibited by infants (with infant-ones having the largest deviations of expected from observed compositions) is corrected by :

$$\text{Corrected estimate} = \text{observed \%time clinging} \times \frac{\text{Proportion of infants in troop}}{\text{Proportion of infants in scans}}$$

therefore for the annual budget:

$$\text{Corrected estimate} = 7.9 \times \frac{17.8}{15.6} = 9.0\ \%$$

Therefore, this procedure suggests that a more accurate estimate for clinging in the annual budget would be 9.0% and not 7.9%. An upward correction of 1.1% would have small repurcussions on the proportions of other activities but is unlikely to be sufficient to determine variability.

However, as noted above, in March there were considerable deviations of expected from observed representation for adult females and infant-ones. All clinging in March was performed by infant-ones and therefore a corrected estimate for this class can be derived using the above formula :

$$\text{Corrected estimate} = 17.0 \times \frac{28.0}{19.4} = 24.5\%$$

Therefore, it is calculated that the under-representation of infant-ones in March under-estimated clinging by 7.5%, a considerable difference. Consequently, activities performed by the over-representated adult females, such as feeding and moving, are probably over estimated in the March budget.

A further confounding factor arises from changes in troop composition due to maturation, births and death and migration. The proportion of infants and juveniles present in the troop varied from 11.3

% in November to 29.0 % in March. With activity budgets of adults and immatures disparate (Fig 7.4) such differences could confound any intermonthly variation resulting from environmental influences.

Marsh (1981a) investigated the influence of this effect by breaking down the aggregate monthly budget for one activity into the estimated proportion of time each class spent in that activity weighted by the proportion of records contributed by each age/sex class :

$$P_n = \sum (P_i \times M_i)$$

where P_n =proportion of the troops aggregate budget spent in a given activity in a given month.

n =number of age/sex classes distinguished

P_i =proportion of time spent in the given activity by age/sex class i for a given month.

M_i =proportion of records in the monthly sample contributed by age/sex class i.

This method was used to dissect the November budget:

$$P_n = (0.433*0.067)+(0.450*0.640)+(0.429*0.169)+(0.388*0.050)+(0.191*0.063)$$

$$=0.421 \text{ or } 42.1 \%.$$

If we assume that the proportion of time spent feeding by each age/sex class in March was the same as in November we can calculate the expected aggregate troop feeding budget. Substituting in the above equation November (with minimum number of immatures) feeding time and March (with maximum number of immatures) age/sex class proportions:

$$P_n = (0.433*0.045)+(0.450*0.543)+(0.429*0.122)+(0.388*0.096)$$

$$=0.352 \text{ or } 35.2 \%$$

Therefore the observed changes in troop composition between these two months, without changes in the activity budget, would be expected to produce a shift of 6.9 % in the time spent feeding in the aggregate budget. With a maximum intermonthly difference in feeding time of 30%, artifacts of this magnitude, could have a major influence on the aggregate budget. In view of such biases bedevilling the troop budget, intermonthly variation in the aggregate budget is compared with the variability shown by the component age/sex classes (see 7.3.2).

C/ Diurnal variation in sample size.

A further bias may arise from a combination of diurnal variation in activity patterns and sampling intensity. As shown in 7.3.2 there was diurnal variability in activity. Diurnality in sampling intensity may result from variation in visibility (lower at dawn and dusk), in observer search effort during scans and in the distribution of scans through the day. Variation in the diurnal distribution of number of records and scans per half hour time interval for the lumped twelve months of data is shown in Fig 7.2. There is a marked tendency for sampling intensity to be lower at dawn and dusk with little variability in the intervening hours. Most of the temporal variation in the distribution of records is due to differences in the distribution of scans (see Fig 7.2). The distribution of the latter is only affected by daylength (i.e. only 2 months with 05.30 scans because in all other months dawn occurred after this time). However, if for each time period the mean number of records per scan is calculated, the first two and last time periods are shown to have been sampled at about two thirds the intensity of the remainder of the day. This variation in sampling intensity, probably due to poor visibility at dawn and dusk, is confined to a small part of the sample and bias is unlikely to have influenced overall activity budgets.

Two other possible sources of bias should be mentioned. Firstly, Marsh (1981a) concluded that the most likely explanation for changes in the recorded activity budget of adult female red colobus was a gradual increase in habituation by this class to the observer. There is no evidence for such bias for "C" troop (Chapter 6) and the degree of habituation appeared to change little. Secondly, if there is between-month variability in the observation schedule, such that there are large variations in the spread of 'follows' within months, as inherent in Clutton-Brock's (1972) data, bias could arise because of differences in the diversity of data collected between months. As pre-scheduled regular sampling was used with "C" troop this problem should not occur.

7.3.2 MONTHLY VARIATION AND AGE/SEX CLASS BUDGETS.

During a langur's life history, activity budgets would be expected to vary as a result of factors such as pregnancy, lactation and maturation. Annual budgets for each sex/age class are shown in Fig 7.4 and Table 7.A. Adult male and female budgets were very similar with substantial differences only for allogrooming and social behaviour. Sub-adult females tended to move more and spend less time inactive than adult females. Juvenile females moved more, allogroomed less and spent less time inactive than sub-adults. Immature budgets differed profoundly from those of adults, with clinging dominating infant's activity. This form of inactivity contributed 81.6 % of the infant-one budget. Therefore, for langurs older than one year, budgets were similar; there were no large differences in the time spent feeding between different sexes or ages.

The monthly variation in aggregate troop budget is plotted in Fig 7.3. The most striking result is the variability in time spent feeding, from 12.6% in June to 42.8% in November with a mean of 22.8%. The G-Test (Sokal & Rohlf 1969), as used by Struhsaker (1975), demonstrated that intermonthly variation in percentage of time spent feeding differed significantly from the expected. The expected distribution was the mean of the monthly budgets ($G=122.66, df=11, p<0.001, \hat{f}_i=22.8$). The intermonthly change was consistent and gradual with considerably more feeding time in the winter than during the hot weather, with the monsoon months intermediate. Such variation is suggestive of seasonality. However, the implication of this from one year's data is presumptive. Checking with data collected February and March 1981 and April to June 1980, not presented here, does indicate between year consistency in monthly budgets and hence seasonality.

However, is this seasonal variation in feeding time real ? In 7.3.1 the influence of changing troop composition on the aggregate activity budget was thought to be an important determinant of variability. However, monthly variation in the % time spent feeding for the aggregate budget and for each langur class older than one year, plotted in Fig 7.8 is very similar. Immature and female budgets could be confounded by maturation and fluctuations in reproductive state (Marsh 1981a) whilst the adult male budget would be expected to be relatively free of such complications. Nevertheless all plots show very similar trends, indicating that variation in feeding time is not a product of troop composition changes.

The visibility bias would have been expected to dampen rather than exacerbate the variation in feeding time. During the hot weather the visibility of feeding animals, feeding predominantly on fruit in the terminals of sparsely leafed canopies, is good whilst it is poor for inactive langurs, who tend to shelter in the shade of the tree core. In contrast, during the cold weather visibility of feeding langurs, feeding predominantly on leaf throughout fully leafed canopies, is poor whilst it is good for inactive animals, which spend more time inactive in open view. Therefore, visibility bias would be expected to overestimate the proportion of time spent feeding in the hot weather and underestimate in the cold weather, i.e. oppose and dampen the trends apparent in the data. Clutton-Brock (1974b) found a similar effect in red colobus.

Therefore, the variation in feeding time cannot be regarded as a visibility arfefact and will be further discussed in Chapter 10.

Variation in time spent feeding is compensated for by inversely related changes in time spent inactive. Time spent moving showed little variation and the proportion of time spent clinging reflected the number of infants present in the troop and their stage of maturation.

7.3.3 DIURNAL VARIATION.

Langur activities were not found to be evenly distributed throughout the day. Fig 7.9 illustrates the diurnal variation in inactivity, feeding and ground movement for one month per season. The distribution of time spent feeding for every month,with months grouped by season, is shown in Fig 7.10. A lumped annual budget of diurnal variation has not been constructed because of daylength variability.

The most striking feature of the variation in feeding activity is the contrast between the hot weather and the rest of the year. From March to May the distribution approximates to a curve with the maxima at dawn and dusk and the minima at noon. There is considerable intermonthly consistency. In contrast, feeding activity in other months is considerably more variable both between months and between hours. The general level of feeding is also lower in the hot weather.

This seasonal contrast is also shown by inactivity and ground moving (Fig 7.9). In May variation in inactivity tends to be the inverse of the feeding distribution with minima of inactivity at dawn and dusk. Ground movements tend to be most pronounced in the early morning and late afternoon. In other months these activities show greater variability in their timing. Also the coldest of the winter months (December to February) show a inactivity peak at about 08.00-08.30 hours, not apparent in other seasons. This channelling of activity diurnality into uniformity in the hot weather in contrast to erratic patterns at other times will be discussed in 7.4.

7.3.4 ACTIVITY HEIGHTS.

Langurs spent a mean of 33.1 % of the daylight hours on the ground over the annual cycle. The intermonthly variation, plotted in Fig 7.11, suggests a tendency for langurs to be more terrestrial in the hot weather than in most of the monsoon months.However, the highest (57.2 %) and lowest (17.9%) degrees of terrestriality are shown by adjacent months (October and November respectively). The annual and monthly distribution of langur heights recorded in 5m blocks during scans is also shown in Fig 7.11. The lower (5-10m) and middle (15-20m) forest levels tended to be utilized most frequently with the middle and high (25-35m) levels used little, apart from in the winter. The upper storey (>35m) was used only from August to November. Over the entire year the most frequently used height class was between 5 and 10m with 17.0% of observations.

7.4 ACTIVITY DISCUSSION.

The tests for bias in the data, though primitive, suggest that the scans gave a realistic impression of langur activity budgets. With a technique such as scanning, bias is inevitable when used with leaf monkeys. However, as Clutton-Brock (1974b) concluded, they are 'unlikely to have affected estimates made in any month by more than 10 % '. However, further investigation of methodological bias in field primatology, especially by the concurrent use of two or more techniques, as used by Oates (1977a) and Marsh (1981a) is desirable. The techniques appear sufficiently robust for the gross differences found here in langur activity, to be regarded as biological reality and not methodological artefacts.

Activity budgets are available from four other langur study sites and the most pertinent activity distinction, between time spent feeding and inactivity, is tabulated below :

Site		% Time Feeding	% Time Inactive	Method	Source
*Kanha		27.8	41.9	30 min scans	this study
*Dharwar		44	33	focal animal	Yoshiba (1967)
Gir	April	48	48	15 min scans	Starin (1978)
	July	37	59		
*Singur		30	38	5 min scans	Oppenheimer(1978)
Simla		41.4	39.1	20 min scans	Sugiyama (1975)

[* annual budgets, the rest were for less than one year]

Due to lack of standardization and information, or small and irregular sample distributions, no study is strictly comparable to that undertaken in Kanha. Fieldwork at Singur is probably the most similar to Kanha in terms of methodology and also in terms of time spent feeding. One of the most striking results was the gross intermonthly variation in feeding time, for all age/sex classes, increasing from a minimum during the hot weather to a maximum in the winter. As noted in 7.3.2 the visibility bias would be expected to dampen such a pattern of variation and not cause or exacerbate it. Oppenheimer (1978) found a similar pattern for Bengal village langurs which spent less time feeding in the hot weather and monsoon (25 %) than in the winter (36 %). There was a strong inverse correlation between % of time spent feeding and mean monthly temperature, but the biological significance of such a relationship was unexplained. Starin (1978) found that a troop spent less time feeding in the monsoon than in the hot weather but did not sample in the cold weather. There are no published quantitative data on the activity patterns of all male bands.

Comparisons between the remainder of the activity budget are complicated by differences in the definition of categories. Variation in the frequency of play and clinging reflects the proportion of immatures in the troop. For moving, Yoshiba (1967) found 6.0 %, Oppenheimer (1978) 9% (8-11% range) and Sugiyama (1975) 6.2 %, in comparison with 13.1 % (10.3-17.8) found in this study.

Langurs of "C" troop spent 7.6 % of the daylight hours, or approximately an hour a day, grooming other individuals or their own pelage:a considerable time investment. This is interesting in relation to the finding of Rajoagopalam & Anderson (1971) that 72 % of langurs and macaques in the outbreak area of Kyasanur Forest Disease of south India were infested with ticks, with up to 135 ticks per monkey. Ticks are vectors of this disease (an arbovirus) and Boshell (1969) implicated langurs as important 'amplifiers' of the virus cycle, which results in some 5 % human mortality and extensive langur mortality. With langurs having the ability to remove such potentially dangerous parasites during grooming, how do large tick loads accumulate?

The annual activity budgets of adult males and females were very similar with only allogrooming and social behaviour substantially different. In particular, there was no apparent difference in the proportion of time spent feeding between adult males and females. The most common pattern in primates appears to be for adult males to spend less time feeding than females (Clutton-Brock 1977b). These differences may arise as a byproduct of sexual dimorphism, as a result of the costs of pregnancy and lactation to females, or as a result of selection favouring individuals who avoid intra-specific competition (Clutton-Brock 1977b). Males were found to spend less time feeding in red colobus in both Clutton-Brock's (1974b) and Marsh's (1981a) studies and in Waser's (1977a) work on the mangabey (C.albigena). However, Harrison (1983c) found that male Senegalese green monkeys (C.sabaeus) spent more time feeding than females. Kanha field observations suggested that differences in male and female behaviour existed, with males most frequently engaged in encounters (see Chapter 8). Males are also of larger size and are without the burden of pregnancy, lactation and infant transportation. Differences in activity budgets were therefore expected. However, as demonstrated by Hladik (1977) for langurs, feeding time is not equivalent to the quantity of food ingested due to variation in food item size and feeding rate. The larger canine size, buccal cavity and jaw musculature of males may allow them to ingest larger quantities per unit time or give them access to food sources denied to females or immatures. Similarly, adult males, by virtue of their size, may be excluded from some tree terminals or alternatively they may gain access to preferred feeding places through intratroop competition. Therefore, although no differences in feeding time investment could be detected between sexes, there may well have been sexual dimorphism in the quantity of food ingested.

Diurnal variation in time spent feeding showed an erratic and inconsistent pattern in the winter and monson. However, during the three hot weather months, diurnal fluctuations are smoothed and consistent with feeding activity occurring predominantly before 10.00 hours and after 15.00 hours. Starin (1978), in comparing a hot weather with a monsoon month, found a similar seasonal variation in diurnal patterns. This entrainment of activity would seem most likely to be the result of inhibition of feeding at the high noon temperatures, up to $42^{o}C$, during the hotter months. With many tree canopies leafless at this time of year feeding at noon is likely to result in overheating and so might be expected to be confined to the cooler hours.

Temperature variation may be the common factor entraining activity cycles in hot weather environments. The through-put of food and timing of digestion are also likely to be important determinants of the timing of feeding during the day, especially in species with ruminant-like digestive physiology (Clutton-Brock 1977b). Temperature is probably also involved in the peak in early morning inactivity in the cold months of December to February when langurs ascend to the canopy tops to bask in the rising sun after the near freezing nights. Short heavy rain disrupted feeding but, if prolonged, langurs would re-emerge from cover to feed. Vegetation provided little effective cover from the intense monsoon rain, after the canopy had been wetted, so the interruption of foraging was probably not out-weighed by any extra chilling resulting from exposure to heavy rain. In the hot weather immature animals occasionally rested in hollowed out trees, wherein the air temperature was probably slightly lower than the ambient.

Though langurs spent about one third of the daylight hours on the ground, this peaked dramatically in October as a consequence of extensive feeding on the seeds of the dominant shrub _Flamengia semilata_. The tendency to use the higher levels of trees in late monsoon and winter may be a result of feeding on mature leaves, especially from larger trees (see Chapter 9). Vogel (1977) summarizes the degree of terrestriality in langurs and the Kanha data fall within the range for peninsular forests (20-50 %). In the open village areas ground use can reach 70-80 % of daylight hours.

Presbytis entellus is one of the most terrestrial of colobines. The congeners _P.johnii_, _geei_, _phayrii_, _pileatus_ and _senex_ are all pre-eminently arboreal, rarely descending to the ground (Roonwal & Mohnot 1977). The Malaysian _P.melalophos_ and _obscura_ appear to be exclusively arboreal (Curtin 1980) but _P.cristatus_ 'may also spend considerable time on the ground' (Roonwal & Mohnot 1977). Similarly, East Africa colobines tend to be arboreal with both Struhsaker (1975) and

Clutton-Brock (1972) observing that red colobus rarely descended to the forest floor. However, Struhsaker (1975) noted that red colobus living in Senegalese savanna often descended to the ground. Oates (1977a) found that a troop of black and white colobus became terrestrial every 2-4 weeks to feed on herbs at pool margins.

The unusual semi-arboreal (or semi-terrestrial) nature of *P.entellus* is, with dietary and climatic adaptability, perhaps related to their wide geographic distribution within south Asia and across habitat types (Hrdy 1977b). The four more specialist congeners, with which *entellus* shares its range, are almost entirely arboreal, conservative in diet and habitat. The anatomy of *Mesopithecus*, one of the most ancient of colobines, suggests a terrestrial adaptation in a rather open environment in Europe and Asia (Hrdy 1977b). The arboreality of many *Presbytis* species is therefore likely to be secondarily evolved from more terrestrial forebears. The adaptability of *entellus* to ground use has meant that it has maintained most of its distribution despite widespread recent deforestation.

7.5 ACTIVITY PATTERNS : SUMMARY.

1/ The proportion of time "C" spent in different activities was estimated using 'instantaneous' scan sampling recorded at 30 minute intervals on five contiguous days per month for a year. The alternative methods available and their biases are discussed.

2/ In the annual budget, expressed as the mean of monthly budgets, " C" spent 41.9 % of daylight hours inactive, 25.7 % feeding, 13.1 % moving and 17.1 % clinging, grooming, playing, social and 'other'. The activity was not recorded in 1.9 % of scans. Bias resulting from differential visibility between activities and diurnal variation in sample size were tested for and concluded to be unimportant. Bias resulting from differential representation of age/sex classes was considered to be important.

3/ Time budgets for langur age/sex classes greater than one year old were similar, without substantial differences in time spent feeding.

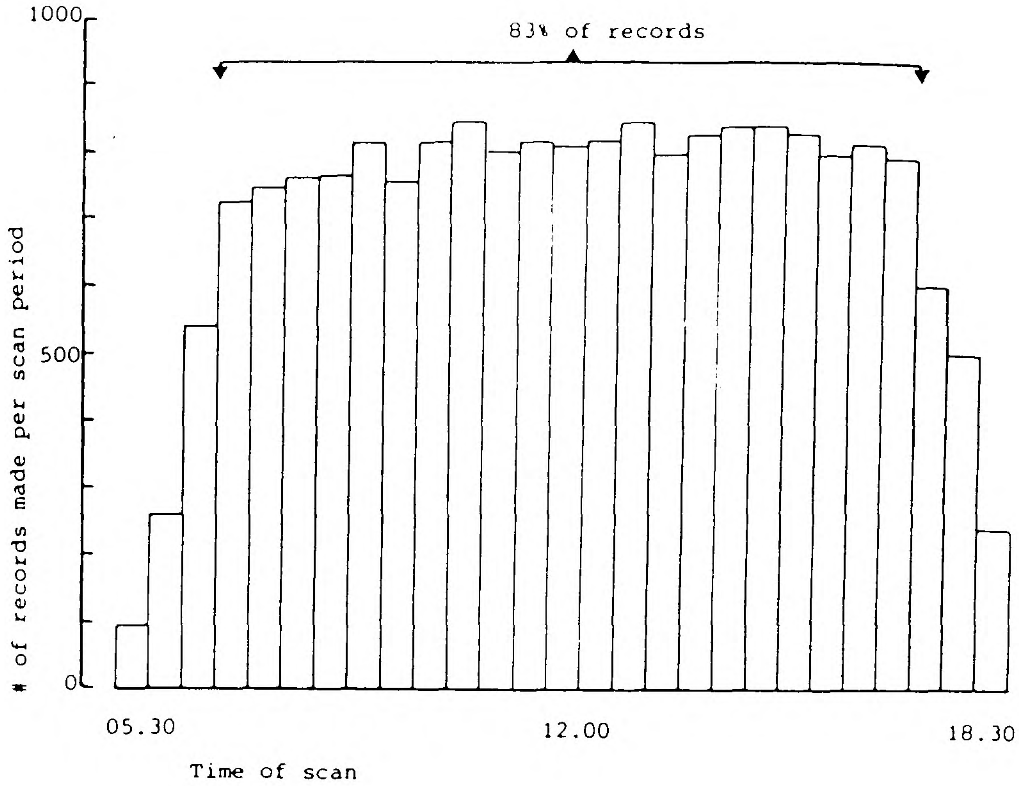
4/ Monthly time budgets, expressed as the percentage of records per activity of the total number of records collected each month, suggested considerable seasonal variation. The percentage of time spent feeding was substantially higher in the winter (max 42.8%) than in the hot weather (max 12.8%).

5/ Diurnal changes in feeding, inactivity and ground movement, variable during most of the year were entrained during the summer months, with feeding largely confined to dawn and dusk, probably as a consequence of high mid-day temperatures.

6/ During the year a mean of 33.1 % of daylight hours was spent on the ground with a maximum in October (57.2 %) and a minimum in November (17.9 %). The most frequently used tree strata were between 5-10 m, with the upper (>25 <35m) levels only occupied during the late monsoon and winter.

The adaptability of *Presbytis entellus* to both terrestrial and arboreal existence may have facilitated its present wide distribution, despite extensive deforestation.

FIG 7.2 DIURNAL VARIATION IN NUMBER OF RECORDS AND SCANS MADE PER HALF HOUR PERIOD (12 months combined).



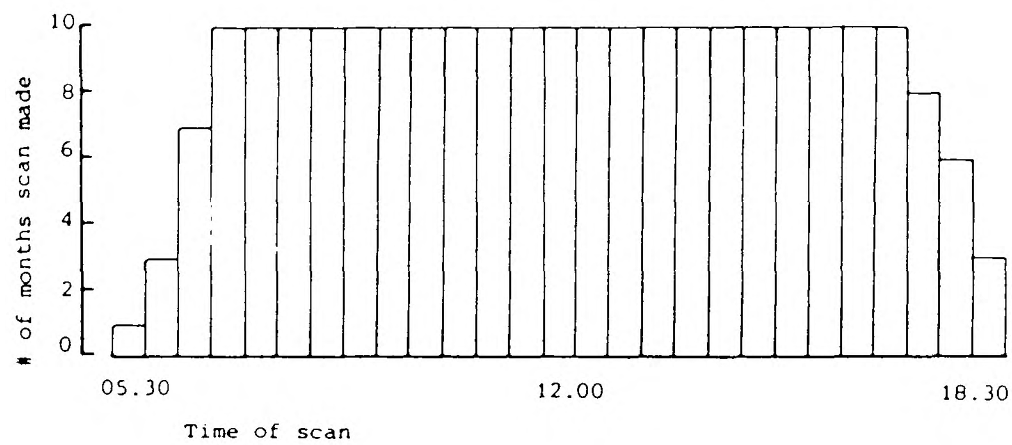
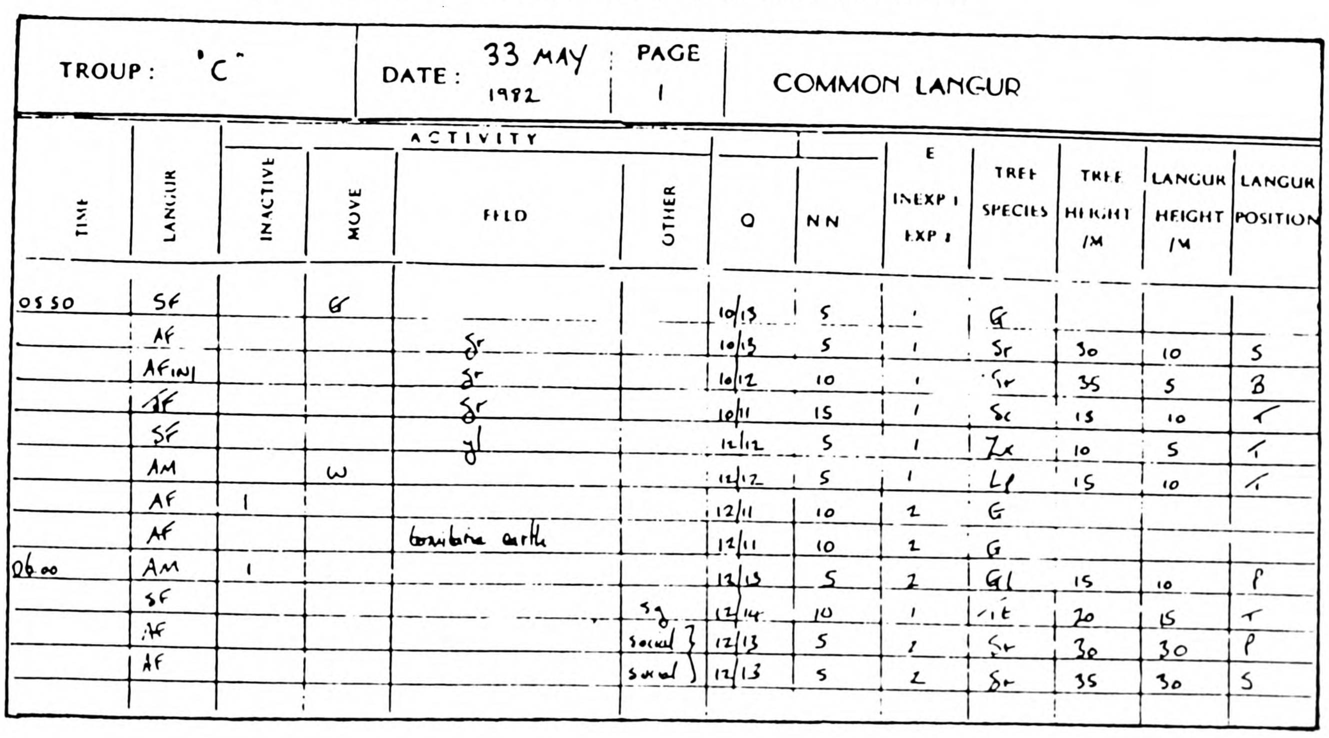


FIG 7.1 EXAMPLE OF CHECKSHEET USED IN SCAN RECORDING.



TROUP: 'C' | DATE: 33 MAY 1982 | PAGE 1 | COMMON LANGUR

TIME	LANGUR	ACTIVITY: INACTIVE	ACTIVITY: MOVE	ACTIVITY: FEED	ACTIVITY: OTHER	Q	NN	E INEXP 1 EXP 2	TREE SPECIES	TREE HEIGHT /M	LANGUR HEIGHT /M	LANGUR POSITION
0550	SF		G			10/13	5	1	G			
	AF			Sr		10/13	5	1	Sr	30	10	S
	AF(N)			Sr		10/12	10	1	Sr	35	5	B
	JF			Sr		10/11	15	1	Sc	15	10	T
	SF			Yl		12/12	5	1	Zx	10	5	T
	AM		W			12/12	5	1	Lf	15	10	T
	AF	1				12/11	10	2	G			
	AF			termite earth		12/11	10	2	G			
0600	AM	1				12/13	5	2	Gl	15	10	P
	SF				Sg	12/14	10	1	[illegible]	20	15	T
	AF				social	12/13	5	1	Sr	30	30	P
	AF				social	12/13	5	2	Sr	35	30	S

FIG 7.3 MONTHLY VARIATION IN "C" TROOP ACTIVITY BUDGET.
ALL SEX/AGE CLASSES.

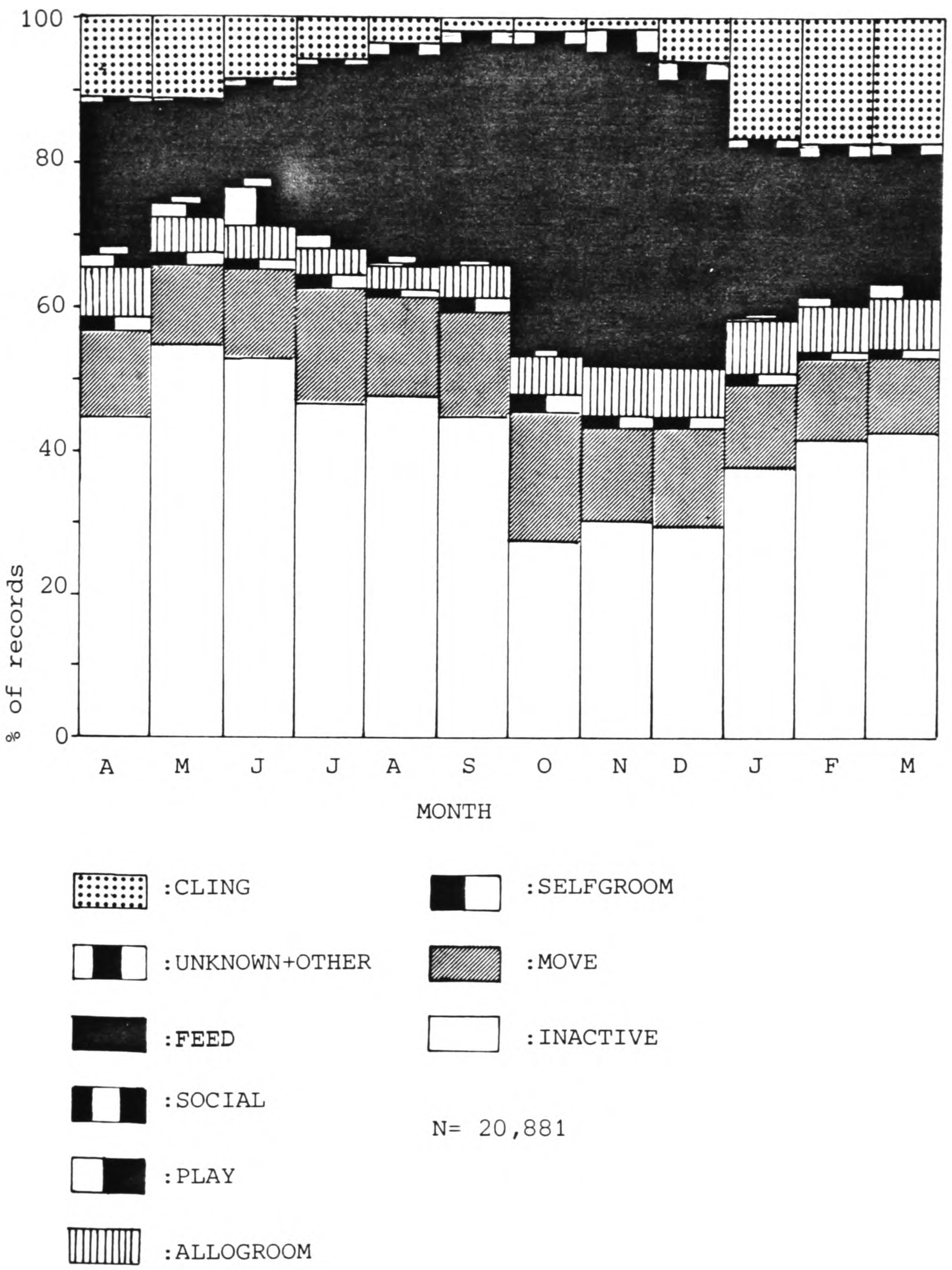


FIG 7.4 ANNUAL ACTIVITY BUDGET FOR "C" TROOP FOR EACH SEX/AGE CLASS.
(Symbols as in Fig 7.3)

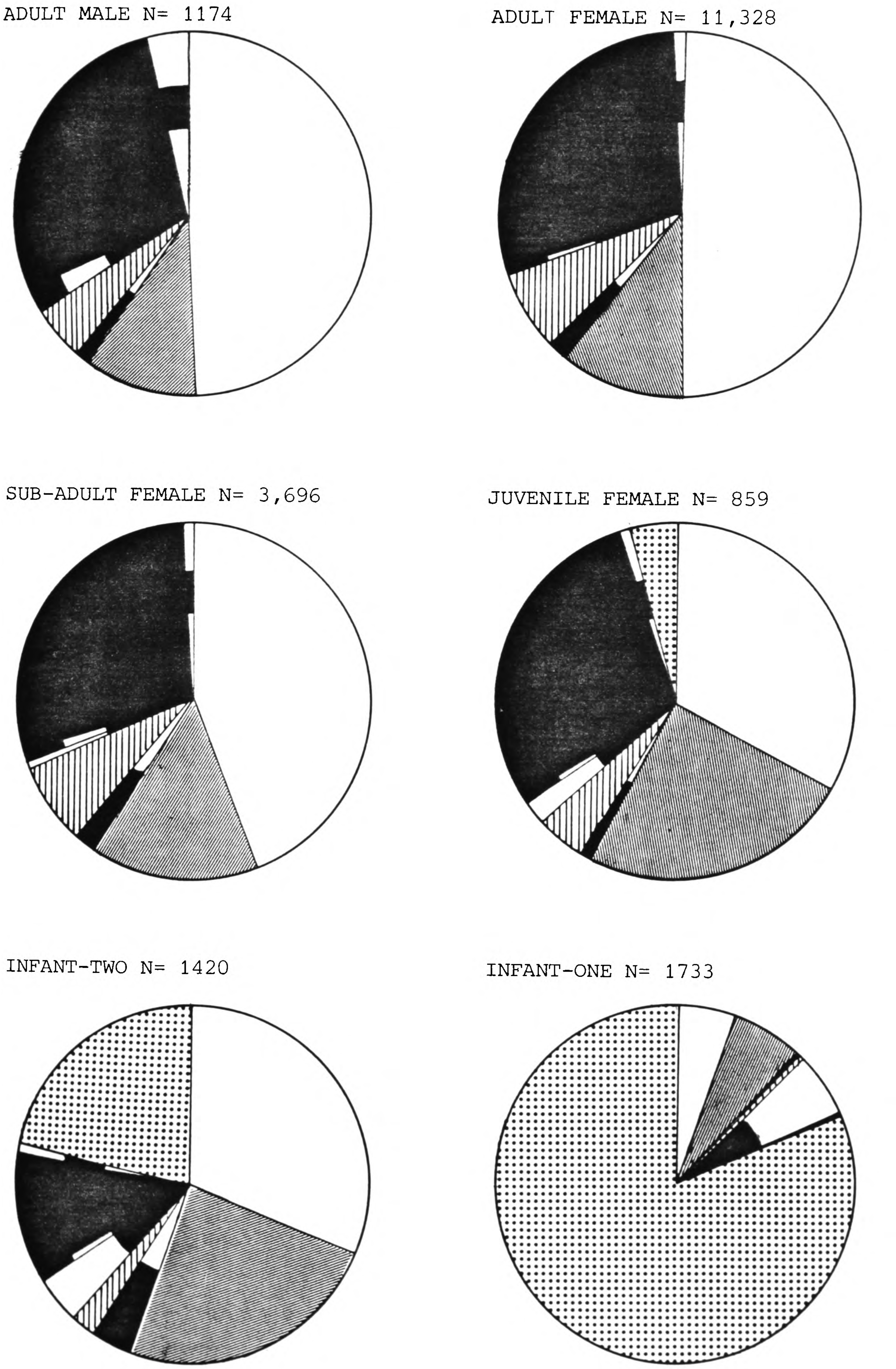
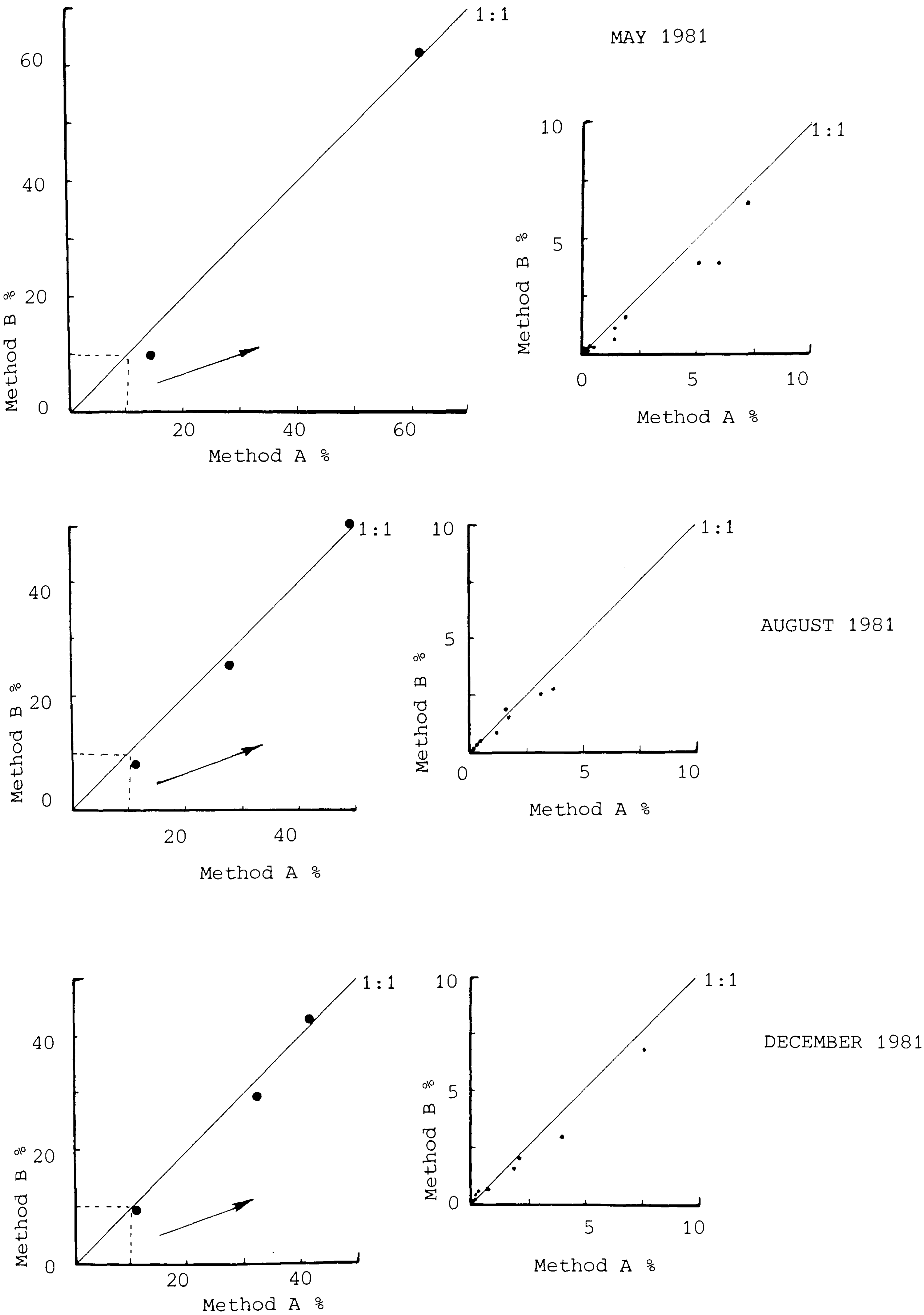


FIG 7.5 TEST OF ASSOCIATION BETWEEN PREDOMINANT ACTIVITY AND VISIBILITY. Comparison of activity budgets calculated by Method A and Method B (see text for details).

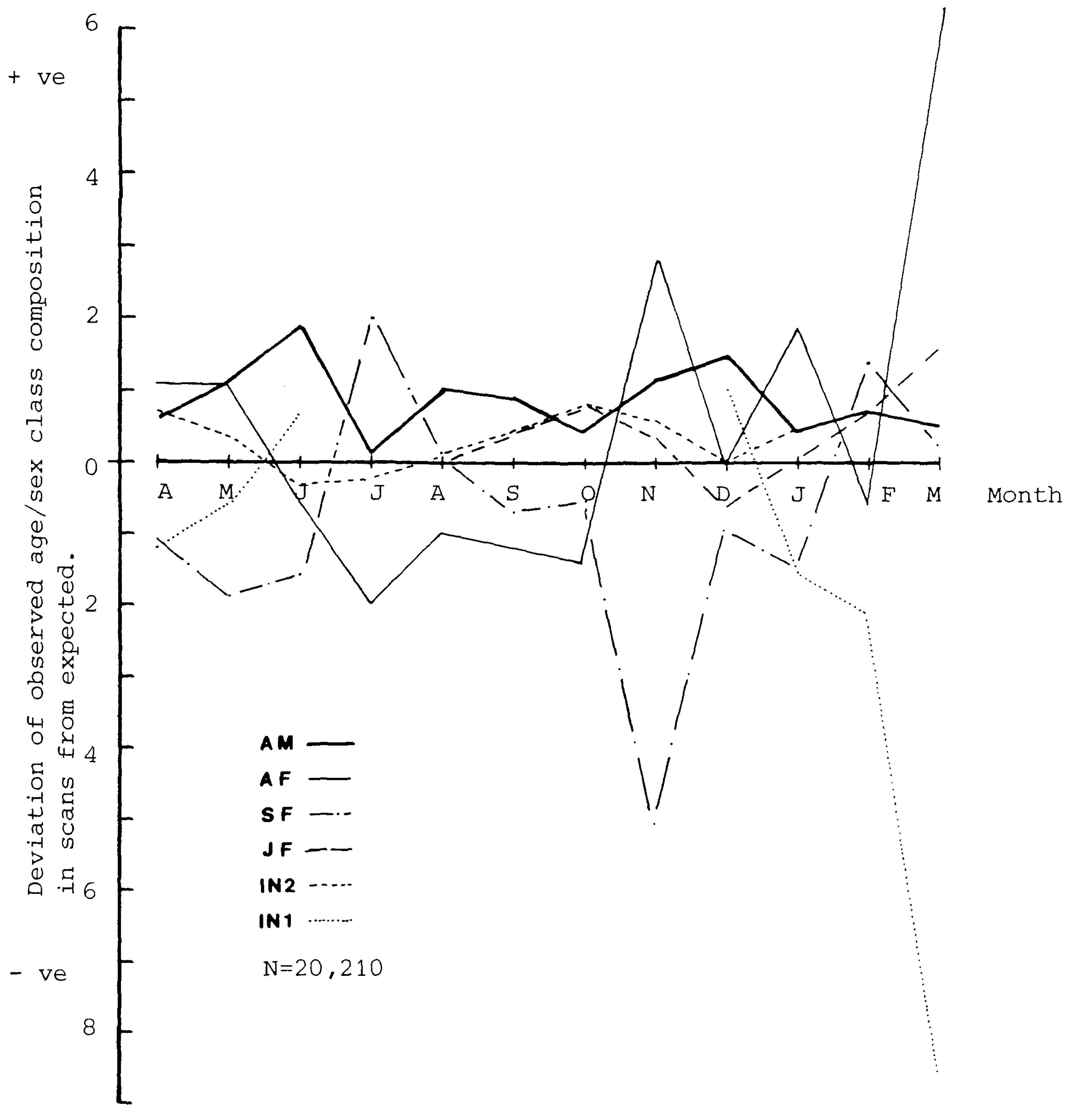


COMPARISON OF OBSERVED AND EXPECTED SEX/AGE CLASS REPRESENTATION IN SCAN DATA (see text).

FIG 7.6 (bottom) FOR ANNUAL BUDGET (12 monthly scan budgets combined)

FIG 7.7 (top) FOR MONTHLY BUDGETS.

(AM=Adult male,AF=Adult female,SF=Sub-adult female)
(JF=Juvenile female,IN2=Infant-two,IN1=Infant-one)



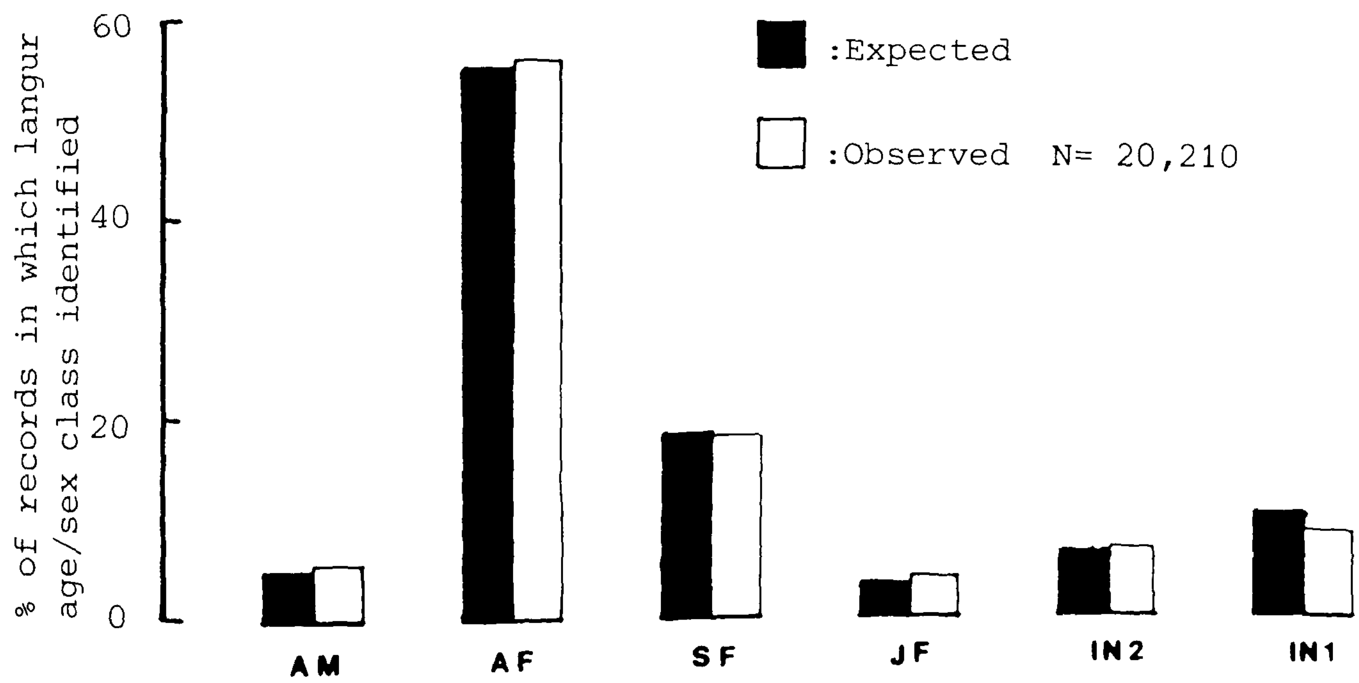


FIG 7.8 MONTHLY VARIATION IN PERCENTAGE OF TIME SPENT FEEDING. FOR "C" TROOP AND CONSTITUENT SEX/AGE CLASSES.

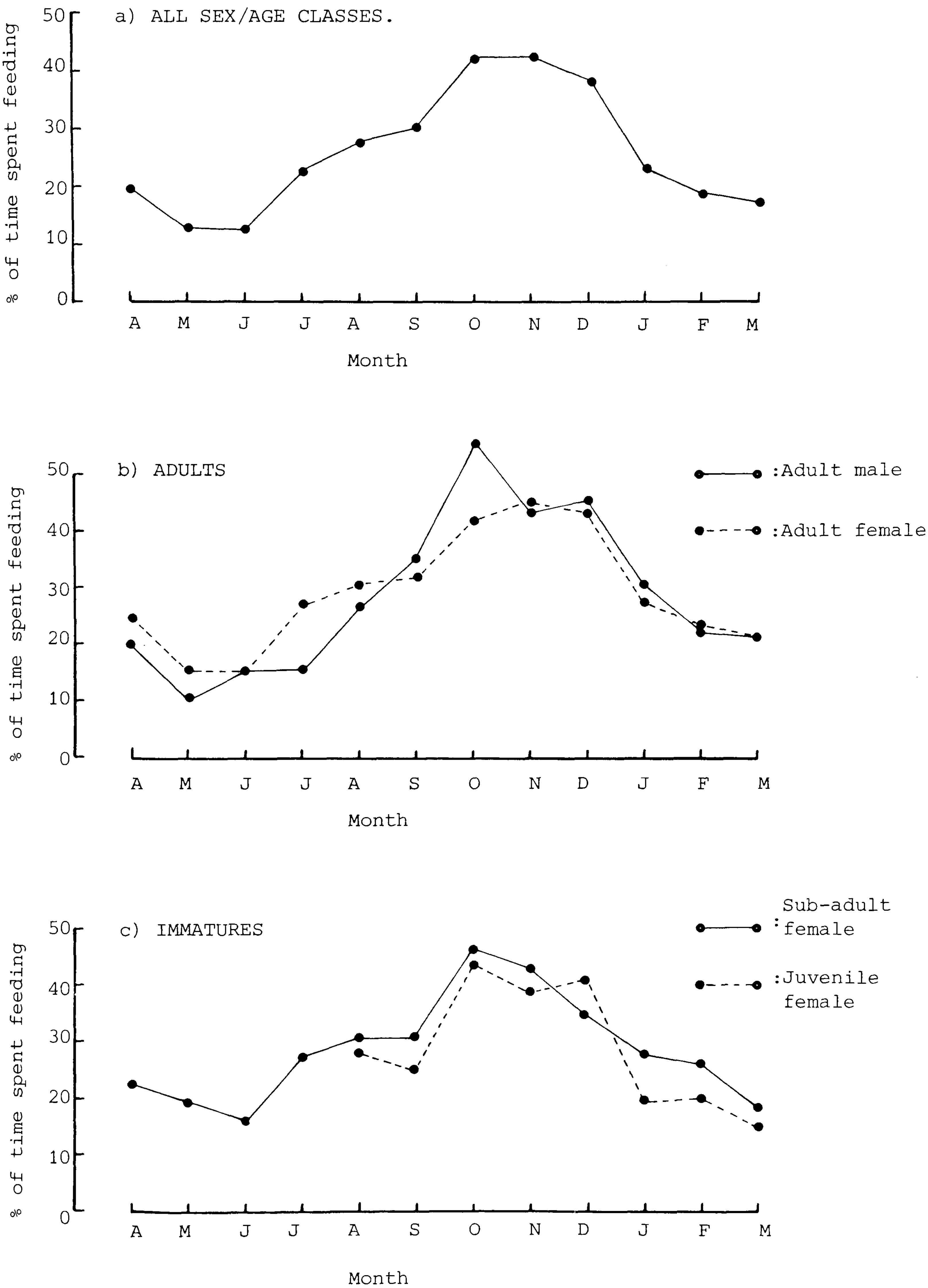


FIG 7.9 DIURNAL VARIATION IN LEVEL OF INACTIVITY, FEEDING AND GROUND MOVEMENT. All age/sex classes.

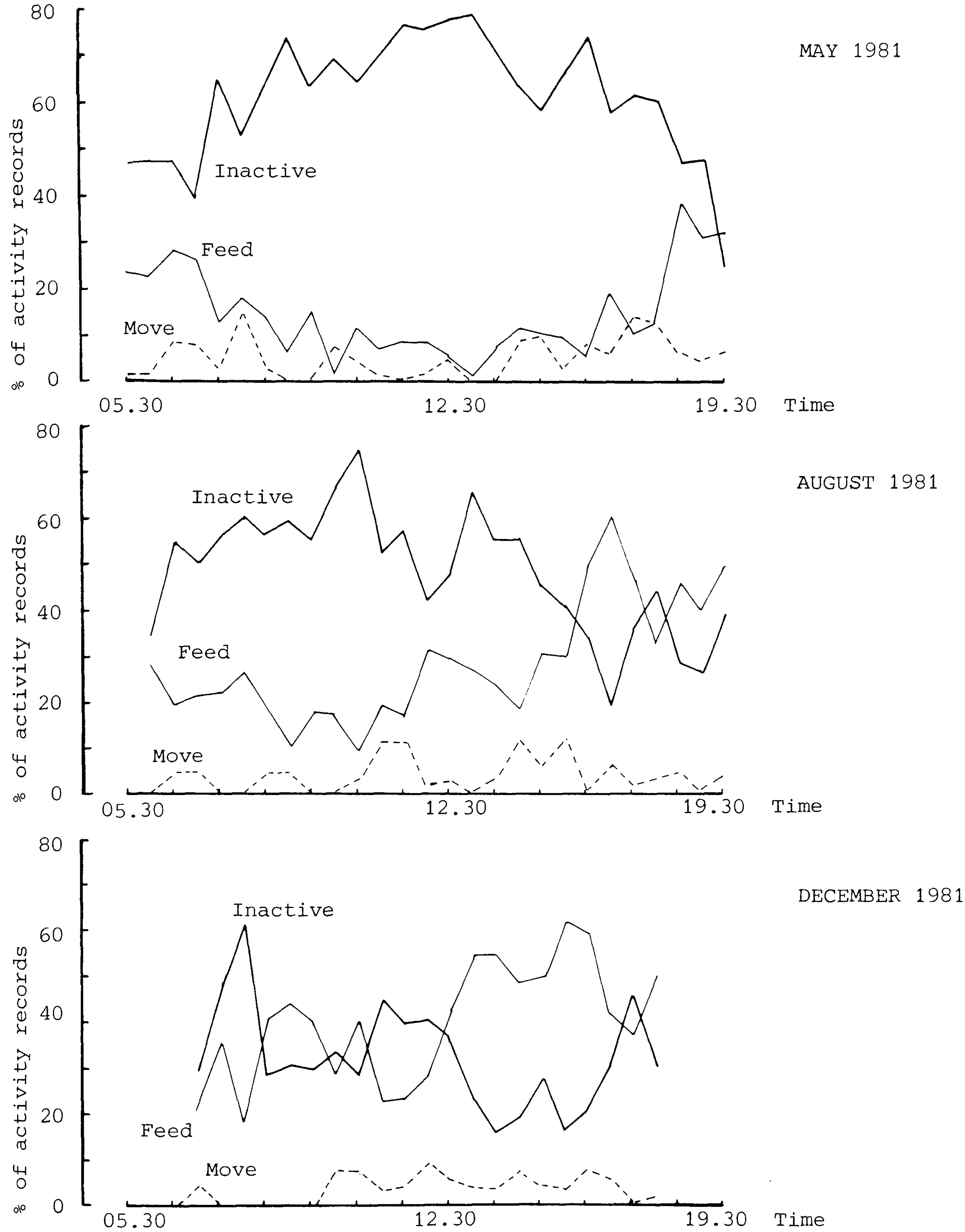


FIG 7.10 DIURNAL VARIATION IN TIME SPENT FEEDING.
All age/sex classes, by seasons.

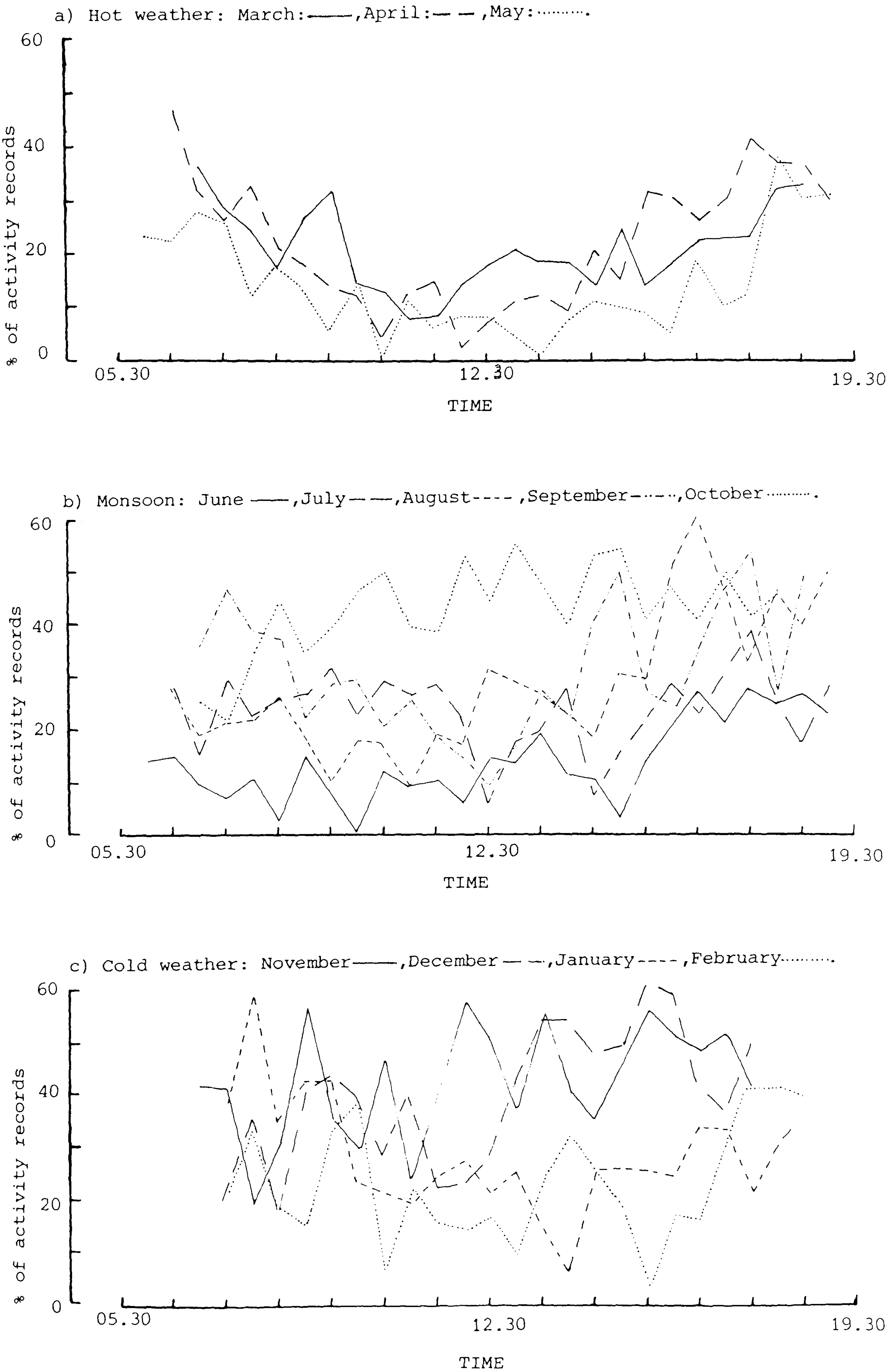


FIG 7.11 MONTHLY VARIATION IN GROUND USE AND HEIGHT ABOVE GROUND IN TREES. "C" TROOP, AS PERCENTAGE OF SCAN RECORDS.(Height in 5m blocks)

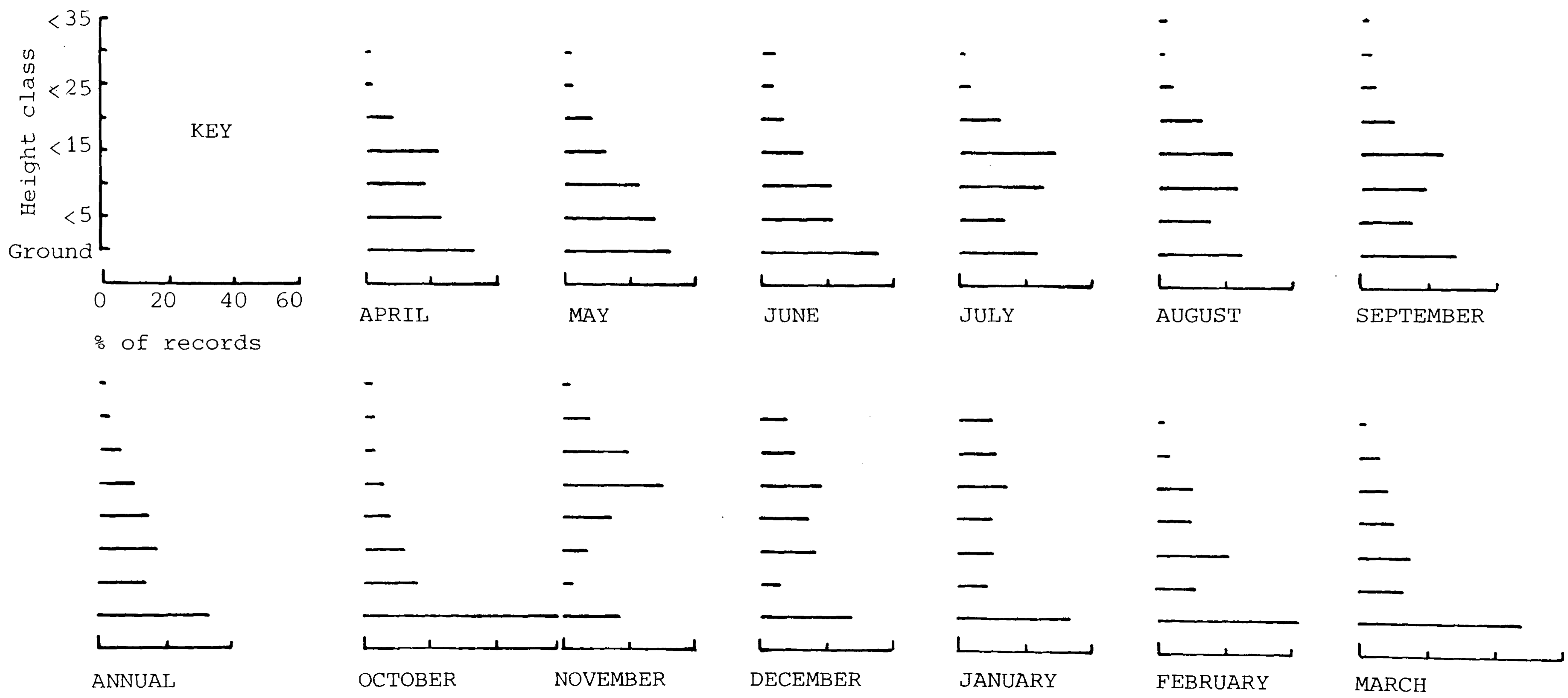


TABLE 7.A MONTHLY ACTIVITY BUDGETS 1981/1982

Abbreviated headings:
Inact. :Inactive
Soc. :Social
Cl. :Cling
XX :Activity unknown
SelfG. :Selfgroom
AlloG. :Allogroom
N :Number of records

Table shows the number of records of langurs engaged in each activity category for 5 days of SCAN follows per month expressed as % of total records collected per month.

MONTHLY ACTIVITY BUDGET : ALL SEX/AGE CLASSES. N=20881

Month	Percentage of records										
	Inact	Move	SelfG	AlloG	Play	Soc	Feed	Other	Cl	XX	N
April	44.7	12.2	1.6	6.9	1.6	1.2	19.7	0	11.2	0.8	1898
May	54.4	11.4	1.7	5.3	1.3	1.2	12.9	0.2	11.1	0.2	2039
June	52.9	12.1	1.5	4.7	5.3	1.3	12.6	0.1	8.7	0.7	1858
July	46.4	16.1	2.1	3.6	2.1	0.5	22.4	0.1	5.5	1.2	1704
August	47.7	13.8	1.1	3.1	0.2	1.5	27.4	0.2	3.3	1.8	1764
September	44.7	15.0	1.7	4.6	0	0.6	29.9	0.4	1.7	1.3	1620
October	27.8	17.8	2.4	5.1	0.1	1.0	42.6	0.2	1.0	2.0	1624
November	30.8	12.7	1.6	6.6	0	0.6	42.8	0.2	1.1	3.5	1445
December	29.7	13.5	1.8	7.1	0	0.7	38.6	0.2	6.4	2.0	1376
January	38.0	11.6	1.5	7.4	0.4	0.2	23.1	0.1	16.1	1.4	1656
February	42.1	11.0	1.2	6.4	0.9	0.2	19.2	0.3	17.0	1.7	1852
March	42.8	10.3	1.1	7.6	1.8	0.2	17.5	0.1	17.0	1.7	2045
Mean	41.8	13.1	1.6	6.0	0.7	0.7	25.7	0.2	7.9	1.9	1740

MONTHLY ACTIVITY BUDGET :ADULT MALE. N=1174

Month	Percentage of records									
	Inact	Move	SelfG	AlloG	Play	Soc	Feed	Other	XX	N
April	55.2	12.4	0	7.6	0	3.8	20.0	0	1.0	105
May	66.4	10.7	2.5	6.6	0	2.5	10.7	0.8	0	122
June	63.7	10.5	0	3.2	0	6.5	15.3	0.8	0	124
July	64.3	11.9	0	3.6	0	3.6	15.5	0	1.2	84
August	57.0	8.4	0	1.9	0	4.7	26.2	1.9	0	107
September	48.5	10.7	0	1.9	0	1.0	35.0	2.9	0	103
October	21.3	16.0	2.1	2.1	0	1.1	55.3	0	2.1	94
November	27.8	10.0	1.1	8.9	0	1.1	43.3	1.1	7.8	90
December	30.7	11.4	2.3	3.4	0	1.1	45.5	4.5	4.5	88
January	48.1	7.6	2.5	6.3	0	1.3	30.4	0	3.8	79
February	54.4	10.0	1.1	3.3	0	2.2	22.2	0	6.7	90
March	55.7	5.7	1.1	9.1	0	0	21.6	0	6.8	88
Mean	49.4	10.4	1.1	4.8	0	2.4	28.4	1.0	2.8	98

TABLE 7.A (contd.)

MONTHLY ACTIVITY BUDGET: ADULT FEMALE. N=11328

Month	Percentage of records									N
	Inact	Move	SelfG	AlloG	Play	Soc	Feed	Other	XX	N
April	52.8	10.2	1.8	8.8	0	0.9	24.7	0	0.9	1053
May	63.8	9.7	2.0	7.3	0.1	1.5	15.0	0.3	0.4	1128
June	65.6	14.6	1.5	5.5	0.1	1.2	14.9	0	0.6	983
July	52.6	12.3	2.5	4.6	0	0.1	27.0	0.2	0.7	878
August	52.0	10.1	0.8	3.8	0	1.1	30.6	0.1	1.5	972
September	48.1	11.2	1.7	4.9	0	0.6	31.6	0.2	1.6	943
October	31.9	14.9	2.6	5.5	0	1.0	41.9	0.2	2.0	938
November	33.3	10.1	1.8	6.5	0	0.4	45.0	0.2	2.7	855
December	34.2	10.1	1.2	8.4	0	0.5	43.8	0.3	1.5	749
January	49.4	11.1	1.5	9.5	0	0.2	27.2	0	0.2	820
February	55.2	9.3	1.4	8.7	0	0	23.5	0.6	1.3	938
March	54.1	10.5	1.4	10.5	0	0.3	21.7	0.1	1.6	1071
Mean	49.4	11.2	1.7	7.0	0	0.7	28.9	0.2	1.3	944

MONTHLY ACTIVITY BUDGET : SUB-ADULT FEMALE N=3696

Month	Percentage of records									N
	Inact	Move	SelfG	AlloG	Play	Soc	Feed	Other	XX	N
April	49.4	12.4	2.5	6.8	3.1	2.8	22.6	0	0.3	354
May	59.5	13.5	1.7	4.1	0.6	0.3	19.6	0.6	0.3	363
June	53.0	13.6	2.7	6.6	5.7	1.2	16.0	0.3	0.9	332
July	45.2	19.3	1.9	4.6	0	0.5	27.0	0	1.4	367
August	47.2	13.5	1.7	3.6	0	1.9	30.4	0	1.7	362
September	40.7	16.8	2.7	7.4	0	0	30.7	0.3	1.2	339
October	23.9	19.2	1.8	6.5	0	1.2	46.3	0.3	0.9	339
November	28.3	14.6	1.3	9.3	0	1.3	42.9	0	2.2	226
December	34.4	16.2	2.4	8.9	0	1.2	34.8	0.4	1.6	247
January	45.5	12.1	3.0	10.2	0	0.4	27.7	0.4	0.8	264
February	47.3	14.1	1.1	8.0	0.4	0	26.0	0	3.1	262
March	54.4	14.5	0.8	10.0	0.4	0.4	17.8	0	1.7	241
Mean	44.1	15.0	2.0	7.2	0.9	0.9	28.5	0.2	1.3	308

TABLE 7.A (contd.)

MONTHLY ACTIVITY BUDGET : JUVENILE FEMALE. N=859

Month*	Percentage of records										
	Inact	Move	SelfG	AlloG	Play	Soc	Feed	Other	Cl	XX	N
August	40.0	23.3	0	0	1.1	2.2	27.8	0	5.5	0	90
September	36.7	28.7	1.1	1.1	0	1.1	24.5	0	7.5	1.1	94
October	14.9	29.7	2.9	4.0	1.0	1.0	43.6	0	2.0	1.0	101
November	31.3	15.0	1.3	7.5	0	1.3	38.8	0	2.5	2.5	80
December	23.0	31.2	0	4.9	0	0	41.0	0	0	0	61
January	38.4	27.4	1.4	5.5	5.5	0	19.2	0	1.4	1.4	73
February	33.5	23.0	0.6	6.5	2.4	1.2	20.0	0	12.4	0.6	170
March	43.7	21.6	1.6	5.3	6.3	0	14.8	0	6.8	0	190
Mean	32.7	25.0	1.1	4.3	2.0	0.8	28.7	0	4.8	0.8	107

MONTHLY ACTIVITY BUDGET : INFANT -TWO (male and female). N= 1420

Month*	Percentage of records										
	Inact	Move	SelfG	AlloG	Play	Soc	Feed	Other	Cl	XX	N
April	30.2	18.9	0	2.8	2.8	0	6.6	0	36.8	1.9	106
May	45.4	21.3	1.9	1.9	0	2.8	5.6	0	21.3	0	108
June	22.6	14.3	0.8	1.9	22.6	0	2.6	0	35.0	0.4	266
July	30.1	19.5	1.5	0.3	10.6	0.9	7.9	0	28.6	0.6	329
August	30.9	28.2	2.8	1.7	1.7	1.1	4.4	0	29.3	0	181
September	43.8	21.9	2.1	1.0	0	1.0	8.3	0	21.9	0	96
October	29.0	22.0	4.0	2.0	1.0	1.0	25.0	0	14.0	2.0	100
November	23.8	33.3	3.6	1.2	0	0	19.1	0	16.7	2.4	84
December	21.8	36.2	11.6	5.8	0	0	14.5	0	8.7	1.5	69
January	32.1	28.5	2.5	4.9	3.7	0	17.3	0	16.1	0	81
Mean	31.0	24.4	3.1	2.4	4.2	0.7	11.1	0	22.8	0.9	142

MONTHLY ACTIVITY BUDGET : INFANT-ONE (male and female) N=1733

Month*	Percentage of records										
	Inact	Move	SelfG	AlloG	Play	Soc	Feed	Other	Cl	XX	N
April	5.4	17.1	1.2	1.6	6.2	0	0.4	0	67.4	0.8	258
May	9.7	10.4	0.4	0.7	8.3	0.4	0	0	70.2	0	289
June	10.7	7.8	0	0	13.6	0	1.0	0	67.0	0	103
December	0	0	0	0	0	0	0	0	100.0	0	82
January	0.7	1.9	0	0.8	0	0	0	0	96.6	0	262
February	6.4	6.4	1.1	0	3.4	0	0	0	82.4	0.3	357
March	2.4	2.6	0.5	0	6.3	0	0	0	87.7	0.5	382
Mean	5.1	6.6	0.5	0.4	5.4	0	0.2	0	81.6	0.2	248

* Juvenile females not present in "C" from April to July 1981.
* Infant-Twos not present in "C" February and March 1982.
* Infant-Ones not present in "C" troup July to November 1981.

CHAPTER 8

RANGING PATTERNS

AND

INTER-GROUP RELATIONSHIPS.

CHAPTER 8 RANGING PATTERNS AND INTER-GROUP RELATIONSHIPS.

8.1 INTRODUCTION.

A major aim of this study was to examine the relationship, if any, between the use of space by langurs, diet composition and the distribution of trees. There is accumulating evidence that such aspects of ecology are related in many primate species (Clutton-Brock 1972, McKey & Waterman 1982, Marsh 1981b, Harrison 1983a). Clutton-Brock (1974a) linked differences in Ugandan red colobus (C.badius) and black and white colobus (C.guereza) ranging patterns to fine variation in feeding ecology and social organisation. Hladik (1977) speculated on similar relationships for Singalese Hanuman langurs and purple faced langurs (P.senex). Across primate species Milton & May (1976) and Clutton-Brock & Harvey (1977) demonstrated relationships between range size, group weight and gross diet type.

Efforts at comparisons between primate ecology and vegetation have been hampered by lack of standardization and by inadequate samples of vegetation composition and phenology (Marsh 1981b). Ranging patterns were investigated in Kanha langurs as part of a constellation of potentially inter-related factors, including total enumeration of trees within "C"'s range and monitoring of the phenology of all species of tree, similar to the integrated study of Marsh (1978). In the first half of this chapter the use of space by "C" troop is described; its relationship to other aspects of ecology is considered in Chapter 10.

The majority of social interactions of "C" animals were within the troop. However, they did not exist in isolation, but interacted with adjacent troops and all-male bands. In the second half of this chapter inter-group relationships are described with the aim of understanding what spacing 'system' (i.e. the behavioural interactions between groups) gave rise to the observed spacing 'pattern' of troops (Waser 1977b). Encounters, considered here in isolation, are integrated with other aspects of langur biology in Chapter 10. Sexual relations between groups and inter-group migration are considered in Chapter 6.3.

Ripley (1967) and Yoshiba (1967) both observed over-dispersed troop range patterns and concluded that langurs are territorial, a suggestion disputed by Vogel (1977). Burt (1943) defined a territory as a defended area and restricted the term to those species that protect all or part of the range, from conspecifics, by fighting or aggressive gesture. Aggression at close quarters is not necessarily implied as vocalizations can be used to repel foreign animals. The definition does necessitate that a specific area should be defended (Chalmers 1979). The definition of Burt (1943) is distinct from Pitelka's (1949) suggestion that a territory is an area of exclusive use (Jolly 1972).

Waser (1977b) pointed out that the spacing 'system', and its manifestation as an observed 'pattern' are not necessarily equivalent and different systems could produce similar patterns. Waser found in Ugandan mangabeys (C.albigena) overlapping ranges with exclusively occupied central areas, suggesting the territorial defence of a specific region. However, Waser demonstrated that mangabeys did not defend their ranges against intruders but achieved the pattern by a system of philopatry and a tendency to avoid neighbouring troops. Using vocalization playback experiments it was shown that troops avoided each other irrespective of location. He concluded that mangabeys showed site-independent intertroop avoidance and not site defence or territoriality. Brown (1964) and Harrison (1983b) suggest that territoriality may be a variable and flexible behaviour depending on whether the benefits of defending an area exceed the costs i.e. on 'economic defendability'.

The investigation of inter-troop relationships among the meadow langurs was designed to reveal which social system underlay the observed over-dispersed spacing pattern. Troops frequently had encounters, usually with inter-group agonistic behaviour such as chases, fights and threats. If langurs are truly territorial, as opposed to showing site-independent avoidance, one would predict that the outcome of encounters (in terms of 'winning') would be dependent on the location of the encounter. If site defence occurred, "C" would be expected to win more frequently towards the centre of its range and lose more frequently towards the periphery (Waser 1977b).

8.2 METHODS.

Range size and utilization was measured using the same grid system as employed in the enumeration of vegetation (see Chapters 3,5). Despite the problems of including lacunae, the use of a grid has the great advantages of replicability and objectivity, not inherent in drawing lines around aggregations of sightings (Altmann & Altmann 1970). Interstudy comparisons are facilitated by the use of a standard mesh size, which has commonly been squares of 50m x 50m (Struhsaker 1975, Marsh 1978, Rudran 1978) for forest cercopithecids. Systematic ranging data were only collected for "C" troop; ad-lib information was collected from adjacent troops. During the monthly seven days of DROP and SCAN 'follows' (see Chapters 3 & 7) "C" was scanned every half hour between dawn and dusk. In each scan the identities of quadrats occupied by one or more langurs were recorded, providing information on the intensity of use of each grid cell by "C". An alternative method, in which the location and timing of movements are recorded (Struhsaker 1975) was not used, because of the difficulties of defining progressions and the diffuse, drifting movement of "C" troop. All data refer to daylight hours, as langurs are very unlikely to change quadrats during the night (pers.obs.). The duration of observation time is shown in Fig 3.1. Additionally, during the DROP, SCAN and ASSOC follows (i.e. 12 days per month), the movements of the central location of the group and of peripheral individuals were plotted onto 1:5000 scale fieldmaps, with sleeping sites and the routes of arboreal progressions mapped. This supplemented the scans by recording the identities of all quadrats entered during the systematic follows, irrespective of whether recorded in scans. Other troops sighted within the study area were identified and the quadrats they occupied recorded.

The potential biases of activity data, considered in Chapter 7, may also influence ranging data as both are derived from scans. However, since quadrats were recorded as occupied irrespective of the number of langurs present in each quadrat the visibility biases are very unlikely to be important. During SCAN & DROP follows the movements of peripheral animals were closely monitored making it very unlikely that occupied quadrats were consistently missed. The changes in troop composition (see Chapter 6) would also have been very unlikely to affect the results, as most changes in the complement were of infants whose movements are dependent on the mother or caretaker.

Encounters between "C" and adjacent groups were recorded opportunistically during the 12 dawn-dusk follows every month. As they are prominent events it is very unlikely that any more than a very few were missed. The terms used are defined below:

Encounter: a state when one or more members of two or more groups were within 50m of each other, irrespective of individual behaviour. If groups separated by greater than 50m and re-engaged <50m within one hour, both periods are classified as the same encounter. If re-engagement occurred after more than one hour, two separate encounters were recorded.

Onset: the time a pair of groups came within 50m of each other.

End: the time a pair of groups separated to greater than 50m.

Initiator: the group whose movement first brought the two groups less than 50m apart at the onset of an encounter.

Terminator: the group whose movement first brought the two groups greater than 50m apart at the end of an encounter.

Initiators and terminators were judged from relative speed and direction of movements. Joint initiation (or termination) was recorded when both troops converged (or diverged) at approximately the same speed.

Outcome: a group was designated the winner if the opposing troop unilaterally increased the distance which separated the groups (Oates 1977b). This could arise by the winner supplanting the opposition or by resisting the advances of the opposition which subsequently withdraws. If no clear outcome could be observed the encounter was recorded as neutral. The loser therefore differs from the terminator as the outcome is a relative measure, without the 50 m criterion.

As other troops were less habituated to myself than "C" was, great care had to be taken to ensure that I did not influence the outcome and I, therefore, kept some 50-75m from the encounter. I kept lateral to direction of the encounter so as not to appear to be behind, and hence possibly an 'ally' of "C" from the point of view of the opposing troop.

Like most other colobines langurs have contagious early morning 'loud calls', given by adult males, which in the Hanuman is rendered as a 'whoop' (see Vogel 1973). These would seem likely to be involved in inter-troop relations but are largely ignored in this study, due to shortage of time and facilities to record them.

8.3 RANGING PATTERNS :RESULTS.

8.3.1 ANNUAL RANGE.

Two aspects of ranging patterns are considered here, the size of ranges and the intensity of use or 'utilization distribution' within those ranges (Don 1983). During the annual cycle, April 1981 until March 1982, "C" was observed to occupy 298 quadrats or 74.5 Ha in 138 follows. "C" was not observed outside these quadrats at any time. The annual intensity of range use is shown in Fig 8.1, plotted by the GINOSURF programme (CADcentre 1983) viewed from the south-west and north-east. Intensity of range use is expressed as the mean of the monthly percentage occupancy records per quadrat (see below). Those quadrats occupied during follows but not recorded during scans are indicated. The cumulative area occupied by "C" increased with the accumulation of observation time towards an asymptote after about 70 days (Fig 8.2). The pattern of range use is cone shaped with the most intensively used quadrats those on and around the chattan. There was a sharp decline in intensity towards the periphery of the annual range. The utilization of quadrats was heavily skewed to the use of a few, especially those about Kuloo chattan. As shown in Fig 8.3 half of the occupancy records were obtained from 23 out of the 225 quadrats tallied during scans (the remaining 74 were occupied during systematic samples but not during scans).

8.3.2 HABITAT SELECTION.

The annual pattern of range use can be compared with vegetation structure, assuming no restrictions on range utilization (see 8.4, Getty 1981), to test whether langurs select for or against the habitats present out of proportion to their abundance. If "C" utilized the annual range irrespective of vegetation type, the proportion of time spent in each habitat would be expected to be similar to the habitats proportional representation in the grid. The 225 quadrats "C" entered during scans were classified as sal forest, mixed forest or meadow by the same criteria as used in 3.1.1. The expected distribution of langur occupancy per habitat is equivalent to the proportion of the grid occupied by each vegetation type. The observed distribution of habitat occupancy is the proportion of time spent in the quadrats constituting each habitat. The degree of habitat selection or avoidance can be expressed using Jacob's preference index (Jacobs 1974,Barnes *et al* 1983) calculated as :

$$P_j = \frac{R_i - Q_i}{R_i + Q_i}$$

where R_i = % occupancy records for habitat_i

Q_i = % of quadrats for habitat_i

P_j = +1 indicates selection, P = 0 no preference and P_j = -1 indicates avoidance. The results are tabulated below:

Habitat	**% of quadrats**	**% of occupancy records**	**Jacobs P_j**
Sal forest	70.7	73.7	+0.021
Mixed forest	5.7	21.3	+0.578
Meadow	23.6	5.0	-0.650
N	225	5789	

The results (see Fig 8.4) indicate that langurs occupied mixed forest more and meadow less frequently than expected on the basis of gross vegetation composition. Jacob's preference index suggests that sal forest was utilized in approximate proportion to its abundance. A χ^2 test of the above data, confirmed that the expected proportions differed significantly from those observed (χ^2=57.48,df=2,p<0.001). The preference for chattan forest was also consistently shown between months, as shown in Fig 8.4. In only one month, April, was observed meadow use similar to the predicted.

8.3.3 MONTHLY RANGING PATTERNS.

A/ Range size.

The pattern of range use, or utilization distribution, for each month is illustrated by GINOSURF plots in Figs 8.5-10. Scan sampling produced, for each month, data consisting of the number of scans in which each quadrat was occupied. These are referred to as 'occupancy records', after Marsh (1981b). As "C" troop occupied between one and seven quadrats per scan there are more occupancy records than scans. Monthly intensity of range use per grid cell is expressed as the number of occupancy records for that quadrat as a percentage of the total number of occupancy records collected in each month. The data were expressed as a percentage of the total number of occupancy records, and not the total number of scans, as the latter would sum to more than 100%, clumsy in calculating cumulative occupancy and ranging diversity (Marsh 1978). 'Occupancy records' are distinct from the scan 'records' of Chapters 7 and 9, which refer to particular animals recorded during scans.

The plots illustrate considerable intermonthly consistency with, in every month, the highest frequency of quadrat use in the region of Kuloo chattan. In months such as February and October the troop ranged widely whilst in November "C" was largely confined to the chattan and its environs. An example of a monthly tracing of the route of "C" is shown in Fig 8.11, for December 1981, showing the tendency to concentrate movements within sal forest and make forays into the meadows (compare with Maps 6,7). Sleeping sites were confined to sal forest and "C" troop were never observed to spend a night in the meadow copses or solitary trees.

The rate at which langurs were recorded as entering 'new' quadrats per month, a property of the sampling regime not the langurs, declined with cumulative observation time, tending towards an asymptote between 6 and 12 days. Fig 8.12 suggests that for most months a sample size of 12 follows was sufficient to accurately estimate monthly range size. However, for December, February, March and May the curves suggest that considerable increases in range size might have occurred if sampling had been extended.

As a preliminary to investigating relationships between ranging patterns and other variables the pattern of range use can be summarized into a variety of descriptive indices. In Table 8.A six such measures are listed for each month and a selection are shown graphically in Fig 8.13.

The mean monthly number of quadrats occupied per day and the number of different quadrats occupied per month show similar variation over the annual cycle. In the mid-monsoon and winter months langurs tended to have small ranges but large ranges in June, October, February, March. It was expected, due to differences in observation conditions, that the daily range size would be less for ASSOC than for SCAN follows but Fig 8.13 does not reveal any consistent differences, suggesting that ASSOC follows gave reliable estimates of range size.

B/ Clumping of pattern.

Of particular interest is the monthly variation in degree of clumping of range use and inspection of Figs 8.5-10 suggests differences, with, for example, April appearing more clumped than January.

The degree of clumping has been assessed by Struhsaker (1974) and Oates (1977a) by using the Shannon-Wiener index of diversity H' (Pielou 1969) where:

$H' = -\Sigma\, p_i \log_e p_i$ where n=number of quadrats entered

p_i=proportion of occupancy records contributed by quadrat i.

Variation in H' is shown in Table 8.A and Fig 8.13. H' is significantly correlated with the number of quadrats occupied per month (r_s=0.739,n=12,p<0.01). H' reflects both the number of quadrats occupied and their evenness of use (Harvey 1977).

Rasmussen (1980) in a review of range use analysis techniques, has criticized the applicability of H' and other indices of clumping. H' does not discriminate between differences in the grain (Pielou 1969) of patterns i.e. does not include information on the location of quadrats, and is also sensitive to the number of quadrats on which it is calculated. Rasmussen (1980) derived an index 'RU' which does not have these disadvantages and is the most suitable descriptive measure available for assessing clumping. RU takes into account both intensity and grain of pattern, with the initial calculation of X_i for all possible pairs of occupied quadrats, where:

$$X_i = \frac{\text{sum of intensity of use for quadrats } Q_a \text{ and } Q_b}{\text{distance between centre of quadrats } Q_a \text{ and } Q_b}$$

RU is calculated as the coefficient of variation for all values of X_i as described in Rasmussen (1980). High values of RU will be obtained for patterns in which those quadrats with maximum intensity of use are separated by the minimum distance. Monthly variation in RU is plotted in Fig 8.13, showing considerable differences within seasons but a tendency for the monsoon months to be more clumped than the cold weather which are more clumped than the hot weather months.

C/ Consistency of pattern.

Another characteristic of range use is the consistency of patterns over time or 'temporal stability' (Rasmussen 1980). Correlation coefficients between quadrat utilization intensity pairs in two patterns of range use are commonly used as indices of consistency. However, they are inappropriate when, as in this data, the relationship between the use of quadrats in one pattern and the use of quadrats in another pattern is not linear. A more appropriate index, though suffering from other disadvantages (Rasmussen 1980), is to calculate the degree of overlap between pairs of ranging patterns. Percentage overlap was computed in the manner of Holmes & Pitelka (1968) and Struhsaker (1975), by the addition of shared percentage values for each quadrat for each pair of months. This statistic assesses similarity in quadrat use but not similarity in grain of pattern. According to Rasmussen (1980) there is no index capable of evaluating both characteristics simultaneously. The percentage overlap between months is tabulated in Appendix V.F and monthly means are given in Table 8.A. Range overlap between months was moderate, varying between 57.2 % and 26.2 %. A single-linkage dendrogram (Fig 8.14, polythetic divisive) was constructed, from the overlap matrix, using CLUSTAN (Wishart 1982, with 'Hierachy' & 'Dendrite' procedures) in the manner of Cody (1974). The abscissa on the dendrogram separates the months, whilst the ordinate gives the similarity. The position of junctions on this scale indicate the degree of resemblance between two months. Different methods of dendrogram construction can yield different patterns, but that used here, agrees with the data in Table 8.A in separating April out as a particulary unusual month.The dendrogram shows that most months clustered together, but October, January and especially April were dissimilar.

D/Dispersion.

Dispersion, or the number of quadrats occupied per scan, is shown for each month in Fig 8.13 and Table 8.A. In all months the troop was most frequently spread between two to four quadrats. The maximum number of quadrats occupied at any one time was seven. Intermonthly comparisons suggest that dispersion was very similar in all months with the troop more compact in May and more scattered in April and June. This overall similarity suggests that the variation in range size is due to distance moved, and not to differences in the spread of the troop.

8.3.4 RANGE OVERLAP WITH OTHER GROUPS.

A/Troops.

The range of "C" was overlapped by four neighbouring bisexual troops; "A" in the west, "N" in the north, "L" in the east and "M" in the southwest. Whenever these were sighted during a follow their location was recorded and, if possible, a census taken. Their composition is described in Chapter 6. The number of days each troop was observed in a quadrat is plotted in Fig 8.15 with the annual range of "C" also shown. The frequency with which any troop was observed within "C"'s annual range is shown in a 3-D plot (Fig 8.16) with a plot of intensity of "C" range use (Fig 8.17,same as Fig 8.1) displayed for comparison. The contrast is striking; other troops were almost entirely only observed at the periphery of "C"'s range and the frequency of sighting declined towards the intensively used centre of "C"'s range and from the forest to the meadow (reflecting the paucity of langur meadow use).

The inter-relationships between "C" and adjacent troops are described in Chapter 6 & 8.4. During the 138 follows from April 1981 until March 1982 foreign troops were observed on 88 days (63.8%) within the "C" annual range. Of the 298 quadrats entered by "C", foreign troops were observed to occupy 151 (50.7%). Frequency of occurrence and overlap is tabulated below for each of the adjacent troops :

TROOP	Days observed		Quadrats occupied	
	No.	%	No.	%
"C"	138	-	298	-
"A"	54	39.1	75	25.2
"N"	23	16.7	23	7.7
"L"	26	18.8	47	15.8
"M"	2	1.4	13	4.4
All	88	63.8	151	50.7

However, the details of Fig 8.15, 16 could be complicated by the opportunistic nature of data collection. The sightings of other troops were all initially made from the vicinity of "C" troop, as it was this troop that was being followed. Hence, the location of sightings of foreign troops was probably dependent on the movements of "C". If "C" and the observer were located at one edge of the study area, a neighbouring troop may be able to make an incursion elsewhere into "C"'s range un-noticed, especially if Kuloo chattan was interposed. This effect would have resulted in the proportion of the study area used exclusively by "C" being over-estimated. An additional bias could have arisen if foreign troops avoided the presence of the observer, who was most frequently present in the centre of "C"'s range. However, the adjacent troops were sufficently well habituated to make it unlikely that I influenced their movements greatly. Additionally, foreign troops were never observed within the central area of "C"'s range, despite the large amount of time spent in all parts of the study area, during each month outside of the follows. Kuloo chattan and its environs were therefore used exclusively by "C" with respect to other troops.

B/ All-male bands.

The range of "C" was overlapped by three known all-male bands, "Q", "R" and "S". Whereas troops were resident in the study area for the duration of the fieldwork (but with "C" formation,"B" transmutation,see Chapter 6) bands were transient, only being recorded for a limited series of contiguous months. The number of days each band was observed during follows is shown in Fig 8.17. In contrast to troops, bands were frequently sighted in the centre of "C"'s range and the spatial distribution of band sightings is similar to the annual pattern of intensity of range use by "C".

Of the 138 follows, bands were observed on 40 days within the annual range of "C". These groups were observed to occupy 133 (44.6%) of the 298 quadrats entered by "C". Frequency of occurrence, overlap and the months the bands were observed are tabulated below:

GROUP	Time span	Days observed		Quadrats occupied	
	Observed	No.	%	No.	%
"C"		138		298	
"Q","QZ"	April-July'81 + March '82	17	12.3	76	25.5
"R"	April-July'81	12	8.7	45	15.1
"S"	July 1981	1	0.7	5	1.7
Solitaries	July,August'81	2	1.5	2	0.7
Unknown	May-Sept'81, Jan,March'82	12	8.7	40	13.4
TOTAL		40	29.0	133	44.6

The relationships between "C" and these bands are described in Chapters 6 and 8.4.

The above data suggest that the central portion of "C"'s range, although exclusively occupied with respect to troops, was utilized by bands. However, visits by bands were uncommon and were largely restricted to the period from April until July 1981. Both the solitaries were adult males apparently passing through. Both foreign troops and bands were similarly habituated; my presence is unlikely to have differentially affected ranging patterns. The details of Fig 8.18 may have been complicated by the possiblity, noted above, that the location of sightings was dependent on "C"'s and hence the observers' ranging pattern. This may have resulted in under-estimating the frequency of use of peripheral parts of the study area by bands. However, as this bias is unlikely to have been grossly different between the two types of groups, the dichotomy between "C" spatial relations with bands and other troops is likely to be real.

8.4 RANGING PATTERNS :DISCUSSION.

The annual range of "C" was estimated to be 74.5 Ha. However, such estimates depend on both the duration of the observations and the method by which the area was measured (Marsh 1981b). The decline in rate of entering previously unused quadrats suggests that a year was a sufficiently large sample to estimate range size and that the occupied area is unlikely ever to be much larger. A study of less than 70 full observation days is unlikely to give a reliable range size estimate. The real value of range size is probably significantly smaller as, like plant frequency (Chapter 5), the estimate is dependent on quadrat size. The 74.5 Ha area will include lacunae never or rarely visited by "C" and hence over-estimates actual range size by an unknown amount. Struhsaker (1975) attempted to improve the annual range measurement by weighting it with the estimated proportion of each quadrat occupied. This method does however, potentially suffer from observer subjectivity and lack of replicability.

It is also dependent on the animals moving in compact groups which negates its use with langurs, as the troop may be dispersed over up to 7 quadrats at any one time. Using this method of correction Strusaker (1975) found that measured range size was reduced from 70.7 Ha to 35.3 Ha. Although probably a more realistic value, it is of unknown accuracy and introduces a large element of observer subjectivity.

Rudran (1978), faced with this dilemma with blue monkeys (C.mitis), used three overlain grid systems with cells of 1/4, 1/16 and 1/64 Ha, which yielded ranges of 72.5, 60.8 and 48.5 Ha respectively. Therefore, reducing quadrat size by 1/16, reduced estimated range size by 33%. Marsh (1981b) carried out the same procedure and found a reduction in estimated range size of 48 %. By using a series of nested, successively smaller, mesh sizes it might be possible to use the relationship between cell size and range estimate to calculate an absolute measure of range size. In the absence of such refinements, the range size of 74.5 Ha should be regarded as an index which is comparable with studies using similar methodology.

Two other short term studies have provided estimates of the size of Kanha maidan troop ranges. Kankane (1980) noted, during two weeks of the early hot weather, that two troops occupied areas of approximately 0.75 km^2 each. Lohri & Nagel (1973) investigated langurs in the same block of forest as studied here, in the late monsoon. Measurement of the area depicted in their Fig 1 as occupied by "B" (approximately equivalent to the location of troop "A" in this study) yields a range of 0.722 km^2, larger than "C" during the same season. I also measured the size of "B" range in fifteen follows (May-July 1980) as 0.495 km^2, comparable to "C"'s range size over the same time span. Therefore, the three Kanha maidan investigations suggest that troop ranges are of the order of magnitude of 3/4 km^2.

There has been much discussion of 'core areas' in the primate literature but these are not discussed here due to the absence of an accepted objective definition. Interstudy comparisons of undefined core area size (e.g. Oppenheimer 1977) are unlikely to be reliable. Monthly variation in range size, consistency and clumping of utilization show little consistent pattern; they are considered in relation to other aspects of "C" biology in Chapter 10.

The isolation of April as the month with least similarity to others was largely a result of movements to the SW of the study area, an area which they only visited in this month. This movement, restricted to the adult male and infant-bearing females, occurred during encounters between "C" troop and "Q" band with infanticide and consorting of some "C" females with "Q" (see Chapter 6). The unusual April ranging pattern may therefore have been a consequence of the vulnerable component of "C" removing themselves from the vicinity of the infanticide-prone "Q" males.

Comparison of habitat abundance and its utilization within the range suggested that mixed forest was consistently selected for and meadow consistently selected against, whilst sal forest was used in proportion to its abundance. However, two factors, apart from habitat selection may be involved (Getty 1981,B.Don pers.comm.). Firstly, interactions with other animals may effect range use. Secondly, if certain areas or habitats are preferred or avoided, this will influence the use of other areas or habitats (the 'distance decay function' of Getty 1981). The latter factor may, in particular, be important as a pronounced utilization peak was demonstrated in the range centre and sleeping sites were confined to sal forest. It is possible that the confinement of suitable sleeping sites to tall trees restricted meadow use. If langurs did select for mixed forest it is probably a consequence of the high density and diversity of food trees in this habitat on the chattans in comparison to sal forest and in particular, meadow. Harrison (1983a) found a similar pattern in Senegalese green monkeys (C.sabaeus), which also selected against open habitats. The high degree of meadow use in April was probably a result of occupancy of the meadow area, in the extreme SW of the annual range, away from the infanticidal-prone extra-troop males.

Milton & May (1976) and Clutton-Brock & Harvey (1977) found, in an examination of inter-specific variation, that terrestrial primates tended to have larger ranges than arboreal ones. Larger ranges are expected in open habitats on the grounds that inhabitants are restricted to foraging on a surface, whilst forest dwellers can utilize the resources of a volume. Clutton-Brock & Harvey (1977) and Chivers (1969) also noted that range size may be reduced at high density and suggest that the relationship results from an intensification of intra-specific competition with increased density. The former also found that, as in many mammal species (McNab 1963), larger ranges were associated with large group and body weight, presumably as a consequence of food requirements and food density. From these findings we may predict that in Hanuman langurs :

a/ range size is larger in open habitats than in forests.

b/ range size is larger in low density populations.

c/ range size is larger, the greater the troop size.

Langur troop range size has been extracted from the literature for fifteen study sites (see Map 8) and is presented in Table 6.C and Fig 8.19, grouped by vegetation type. The studies for which range size refers to fieldwork of a year or more, are indicated in Fig 8.19, inspection of which shows considerable variation in troop range size, from 12.5 km^2 in the Himalaya to 0.17 km^2 at Dharwar. Variability can also be large within sites, as witnessed by Junbesi, Simla and Orcha. As noted by Vogel (1977) there appears to be no generally applicable relationship between vegetation type and range size. Although Oppenheimer (1977) and Roonwal & Mohnot (1977) consider that range size is larger in open habitats, the sample used here does not support the suggestion. There is a tendency for Himalayan troops to have larger ranges than peninsular Indian troops (with the exception of Orcha and Kaukori), perhaps as a result of patchiness of resources and winter food scarcity at high altitudes (Bishop 1979). This suggestion is supported by the observation of Sugiyama (1975) that, at Simla, range size was larger in a more severe, high altitude environment.

The relationship between range size and population density (from Table 6.C) is shown in Fig 8.20 suggesting a negative curvi-linear association. Log transformation (base 10) of the data yields a significant linear regression (r_s=-0.735,n=15,$p<0.01$). Similar relationships have been found in other mammals, for example, tree squirrels and microtines (Don 1983). However, as noted by Don (1983) the direction of causality is uncertain; high density may impose small ranges due to competition, ranges may be small because of high food abundance or range size may determine density. It is also interesting that those populations with infanticide recorded (see Chapter 6) consistently have small ranges. A similar association was found by Harrison (1983a) for diverse populations of the super-species C.aethiops. The relationship between range size and mean troop size (from Table 6.C) is shown in Fig 8.21. There appears, contrary to the prediction, to be no clear association. Sugiyama et al (1965) and Sugiyama (1975) found positive relationships within the sites of Dharwar and Simla respectively. Therefore, intra-specific comparison supports the suggestion that range size is related to population density but not to troop size or habitat type.

Little information is available on the ranges of all-male bands and unfortunately no quantitative data were collected in Kanha.

Roonwal & Mohnot (1977) quote band ranges of 7-22 km^2 and Oppenheimer (1977) 10.5-12.0 km^2 for Jodhpur. At Dharwar, Sugiyama et al (1965) recorded a six member band occupying 35 Ha and encompassing at least three troops. The 16.62 km^2 band range, quoted by Oppenheimer (1977) for Dharwar, would appear to be a density estimate and not a range measurement.

Opportunistic evidence from Kanha and many other sites (Roonwal & Mohnot 1977) suggests generally large band ranges, which overlap extensively with troops. This pattern can be interpreted in terms of a dichotomy in reproductive strategy given the troop-band social organisation. The degree of reproductive success of females and the attached adult male is probably dependent on the quantity and quality of available food for successful gestation and raising of offspring. Hence, they occupy defendable ranges, containing sufficient resources; the benefits, in terms of resource availability, exceed the costs, in terms of energy expenditure and risk of injury (Brown 1964,see 8.5,8.6). Such site attachment also promotes familarity with the area and enhances facilitation of gum (see Chapter 9) and of food items by 'pruning' (Oppenheimer and Lang 1968). In contrast, the reproductive success of band males is dependent on the insemination of troop females, either by taking advantage of adulterous solicitations, or by engineering takeovers, to become the stud of a troop. The strategy maximizing individual male fitness in these circumstances might be to range over a large area, to monitor troops for mating opportunities. Without the burden of pregnancy or lactation, nutrition is less important to reproductive success than increasing the probability of successful matings.

The Kanha langur range size estimate is similar to many other published values for colobines studied using a grid system, e.g. for red colobus 114 Ha (Clutton-Brock 1975b) and 70.7 Ha (Struhsaker

1975), for black and white colobus 32 ha (Oates 1977b) and black colobus (C.satanas) 59.5 ha (McKey & Waterman 1982). For Asiatic colobines Roonwal & Mohnot (1977) record ranges of 2-3 ha for P.senex, 5.6-259 ha for P.johnii and 43 ha for P.cristatus. Therefore most colobine populations have annual ranges of the same order of magnitude, with some species, such as black and white colobus and purple-faced langurs, being distinguished by particularly small ranges.

As in the present study, Jay (1965), Hrdy (1977b) and Sugiyama et al (1965) found a difference between the range overlap of troops with bands and other troops. At Melemchi troop-troop overlap was 'moderate' and at Simla and Junbesi 'almost none' (Bishop 1979). At Orcha, judging from Fig 5.6 in Jay (1965), overlap was approximately 20-30 %. Inspection of Fig 4.5 in Hrdy (1977b) suggests that troop overlap was of a similar order of magnitude to that found in Kanha.

Bands were rarely seen to feed within the range of "C", most of their time within the area was spent in encounters with "C" (see 8.5). The frequency of band visits was low. Therefore, in terms of food resources the occurrence of bands probably had little significance. In contrast, adjacent troops commonly fed in the peripheral overlap zone. For "C" troop, the area of exclusivity of use, surrounded by an overlap zone, is coincident with the portion most intensively used. This equivalence of exclusivity with intensivity is by no means mandatory and the two concepts, despite considerable confusion in the literature, are quite separate (Chalmers 1979). Indeed, Oates (1977b) found that 74 % of quadrats occupied by a Colobus guereza troop were shared with other troops, but the exclusively used area was not co-incident with the most intensively used region. There is little quantitive information on group overlap published for other Presbytis species. Roonwal & Mohnot (1977) note that for P.johnii 'considerable portions of the home range overlap'.

Curtin (1980) in Malaysian rainforest found 3 % overlap for Presbytis obscura and 19 % for P.melalophos. Struhsaker (1975), working with C. badius in which bands do not occur, found that three troops overlapped extensively within a 50 ha area to the virtual exclusion of conspecifics.

Therefore, in conclusion, langurs may have selected for the use of the central chattan because of its concentration of food density and diversity. April ranging patterns may have been influenced by the movements of an infanticide-prone band. Intra-specific comparisons suggest that range sizes are smaller at high density. A pronounced dichotomy was found in inter-group overlap: adjacent troops occupied the periphery of "C"'s range whilst bands invaded the centre. This difference is interpreted in terms of a dichotomy in reproductive strategies between troop and band males. The distinction is further investigated in the second half of this chapter, by examining inter-group relationships.

8.5 INTER-GROUP ENCOUNTERS : RESULTS.

During the 138 follows 137 encounters were recorded, 94 with five known troops and 36 with bands, most of which were with either of two known bands. The identity of the opposition was unknown in seven encounters. Therefore, the frequency of encounters per day was 0.99, comprising 0.68/day for troops and 0.26/day for bands. With the primary separation of langur social organisation into troops and all-male bands "C" encounters will be considered according to this division.

8.5.1 TEMPORAL VARIATION.

A/ Monthly variation.

The monthly variation in daily frequency of encounters is shown in Fig 8.22, suggesting that contacts were rarer in the late monsoon and winter than at other seasons. Encounters with bands were most common from April to July, none being observed from September until December inclusive. The troop-troop encounter frequency was consistently higher than for troop-band. The mean daily encounter frequency for each troop is also shown in Fig 8.22. "A" troop had encounters with "C" frequently in June, July and March, but there were very few contacts in other months. "B" was contacted twice in April before its fission (see Chapter 6). "C" had encounters with "L" and "N" most frequently from September until January. The bands "Q" and "R" were frequently encountered only from April until July. The overall pattern for both types of group appears to be that foreign langurs came into contact with "C" only during certain runs of months and were little in evidence throughout the rest of the year.

B/ Diurnal variation.

Each dawn-dusk follow was divided into four equal time blocks and the frequency of occurrence of encounter onset in each block plotted in Fig 8.23. With all encounters pooled, they were most frequent in the second and last quarters of the day. However, troop encounters were most prevalent towards dusk and those with bands during the first half of the day. There was a significant difference between the diurnal distribution of "C"'s encounters with bands and other troops (χ^2=10.107, df=3, $p<0.05$).

C/ Encounter Duration.

The mean duration (end-onset time) for all encounters was 38.8 ± s.d. 53.7 minutes, for troops 33.3 ± s.d. 49.8 minutes and for bands 55.7 ± s.d. 61.1 minutes. Monthly variation in encounter duration is plotted in Fig 8.22. Encounters with troops tended to be longest in the hot weather and late monsoon. The duration of encounters with bands declined steadily from April until September.

8.5.2 LANGUR PARTICIPANTS.

For each encounter an age/sex class was recorded as participating if one or more member of that class was observed as an actor of one or more of the behaviours considered in 8.5.3. The involvement of age/sex classes in troop and band encounters is shown in Fig 8.24.

During troop-troop encounters similar age/sex classes, including females and immatures, were involved from "C" and from the opposition. Adult males were the most frequently represented, clearly participating more often than expected on the basis of troop composition. However, when "C" was opposing a band, "C" participation was largely restricted to the adult male; adult females rarely became involved. From the band, adult males and occasionally sub-adult and juvenile males were involved. There is therefore evidence of a dichotomy in the behaviour of "C" to other troops and towards bands.

8.5.3 BEHAVIOUR DURING ENCOUNTERS.

During each encounter vocalizations and aggressive behaviours were recorded, irrespective of troop identity and frequency. The definitions of categories of behaviour follow Dolhinow (1978) and Vogel (1973). See Roonwal & Mohnot (1977) and Hrdy (1977b) for a general description of encounter behaviour. The relationship between "C" and band "Q" is described in Chapter 6. Vocalizations were heard during 86% of troop-troop encounters and 100% of troop-band encounters. The 'whoop' was the most frequently heard category with 'canine grind', 'squeal' and 'grunt with grimace' also commonly heard (see Fig 8.25). The 'chist' and 'hack' alarm calls were not heard in contacts with bands. No encounter was characterized by vocalisations alone.

Aggressive behaviour between troops was observed in all but 4 of the 80 encounters for which data were sufficiently detailed. These four encounters consisted largely of play between immature animals of both troops. Ritualized arboreal displays were more frequently observed in band encounters than in troop contacts (Fig 8.25). During six encounters 'parallel spats' were noted in which the langurs, mostly adult females, threatened each other, whilst arranged in opposing parallel lines a few yards apart (Hrdy 1977b). The data are of limited value owing to a lack of information on the identity of troops exhibiting the behaviours and because of the simple presence/absence method of recording. However the data do emphasise that the vast majority of encounters were aggressive melees. Band-troop encounters tended to be more vocal, lacked parallel spats and play but had a higher frequency of arboreal displays.

8.5.4 SPATIAL VARIATION.

The distribution of quadrats in which encounters were observed are plotted for troops in Fig 8.26 and for bands in Fig 8.27. As described in 8.3.4, adjacent troops did not occupy the centre of "C"'s range whilst bands did; the spatial distribution of encounters showed a similar pattern. As the majority of neighbouring troops sighted by the observer also came within 50m of "C", the distribution of encounters in Fig 8.26 is similar to that of sightings depicted in Fig 8.15. In contrast to troops, the distribution of band-"C" encounters shows an entirely different pattern (see Fig 8.27). The majority of encounters (and sightings, see Fig 8.17) occurred in the central area of "C"'s range with comparatively few noted at the periphery. There is therefore, a marked dichotomy in the location of encounters between "C" and other troops, and between "C" and bands. Group avoidance or attraction could be tested for by comparison of the observed encounter frequency with that predicted from the probability of encounters occurring by chance, calculated from the range utilization patterns of opposing groups. However, the data on quadrat use are, apart from for "C", insufficient, owing to a probable dependence of foreign group sightings on my movements, and the prediction cannot be tested.

8.5.5 ENCOUNTER OUTCOMES.

As described in 8.2, for each encounter an initiator and terminator was recorded and the outcome judged as a win, loss or neutral for "C". The frequency with which "C" and the opposing langurs initiated, terminated and won encounters is shown in Fig 8.28. The identities of the terminator and loser troop are not equivalent, due to the 50m criterion attached to the former. Frequency differences between "C" and the opposing troop (hereafter "X") are small, but for troop encounters "X" most frequently initiates, "C" terminates and wins. In contrast, for band encounters "C" most frequently initiates, whilst "X" terminates and "C" wins.

Outcomes can be examined in more detail if the sequence of initiation, termination and winning is considered in full. Dendrograms for encounters in which the entire sequence was recorded are presented in Table 8.B and 8.C. If "C" initiated against a troop opponent there was equal likelihood of "C" or "X" terminating. If the latter terminated "C" usually won, whilst if "C" terminated the most prevalent outcome was neutrality. If "X" initiated, "C" was more likely to terminate and "X" win. If "C" terminated, "X" was more likely to win. The summary at the base of Tables 8.B,C shows that the troop which initiated tended to win and the troop which terminated tended to lose.

Turning to encounters with bands, in the sample with the entire sequences known, "X" most commonly initiated (unlike in Fig 8.28), terminated and won. If "C" initiated "X" tended to terminate and "C" win. As with troops, the group which initiated tended to win and the terminator lost.

The encounters can also be broken down by the opposing groups as tabulated below:

GROUP	#"C" WIN	#"C" LOSE	# NEUTRAL	# UNKNOWN	TOTAL
Troop					
"A"	15	14	9	6	44
"N"	8	3	8	0	19
"L"	6	5	6	5	22
"M"	0	2	0	0	2
"B"	1	1	0	0	2
Total	30	25	23	11	89
Band					
"R"	3	2	2	1	8
"Q"	7	5	2	1	15
Total	10	7	4	2	23
Grand total	40	32	27	13	112

"C" consistently won and lost similar numbers of encounters with both bands and other troops, with perhaps a slight tendency for "C" to win more. The difference between frequency with which "C" won and lost encounters was not significant (χ^2=0.09,df=1,p>0.05). About a quarter of encounters were neutral.

As mentioned in 8.1 the spatial pattern of encounter outcomes is crucial to distinquish between site-independent avoidance and site defense 'systems' of spacing. The spatial distribution of those outcomes between "C" and other groups, for which a clear result was evident, are shown in Fig 8.29 and 8.30 as a function of the distance of the encounter from the centre of "C"'s annual range. Distance was measured in quadrats from the most intensively used grid cell (Q 12/13). The pattern for bands showed consistent "C" wins, in terms of supplantation, irrespective of distance. Therefore outcomes did not appear to be site-dependent. The preponderance of "C" wins may, in part, arise because the bands are more mobile and wide ranging, making them more likely to depart the encounter. The differences between the spatial distribution of "C" wins and loses are not significant (χ^2=5.89,df=4,p>0.05). The detail of the distribution does however suggests that "C" tends to win consistently in the inner periphery but that encounters beyond are variable in outcome. The data are therefore equivocal. There is some evidence that outcomes are site-dependent in the central part of "C"'s range, on the rare occasions that troops enter within two quadrats of Kuloo Chattan, but not in the outer periphery. There is, therefore, some inconclusive evidence that the observed over-dispersed pattern of troop ranges is maintained by a system of territorial site-specific defense rather than site-independent avoidance.

In summary, encounters between troops were mostly aggressive and occurred throughout the year, most frequently towards dusk with all post-infant langurs participating on occasions. "C" won and lost similar proportions of conflicts. The outcome of encounters which occurred in the inner, but not the outer, periphery of "C"'s range were site dependent. Troop-band encounters were prevalent only from April to August, most frequently occurring in the morning, with usually the adult male the only participant from "C". All contacts were aggressive with a high frequency of arboreal displays and vocalizations and lacking play behaviour. These encounters occurred mainly in the central portion of "C"'s range and outcomes appeared to be site-independent.

8.6 INTER-TROOP ENCOUNTERS : DISCUSSION.

The investigation of inter-troop relations, through the recording of encounters, suggests an important dichotomy between the relationships of troop with troop and troop with band (no information was collected on band-band relations). Apart from the four play encounters no evidence was obtained to suggest that troop-troop encounters could be naturally subdivided on the basis of behaviour or associated ecological conditions as found by Harrison (1983b) for green monkeys. The contagious whoops given by adult males, especially in the early morning, are probably involved in inter-troop relations, but as encounters occurred daily it seems unlikely that they are part of an avoidance system as found in mangabeys (Waser 1977b).

The arrangement of troop-troop encounter outcomes suggests that the spacing pattern was produced by a territorial spacing system maintained by site-dependent inter-troop conflict at the inner periphery. The consistency of "C" wins on the rare occasions when adjacent troops penetrated close to Kuloo chattan suggests that "C" was actively defending the chattan area. There was no evidence of site-dependent defence of sal forest. A different system underlies the troop-band relationship with no indications of territoriality; indeed bands appeared to seek out a troop in the centre of its range, as shown in Chapter 6.

Jay (1965) working in a similar forest type to Kanha, at Orcha, found an absence of aggressive inter-troop contests but pronounced agonism between troops and bands. Starin (1978) working in the Gir Forest recorded frequent encounters (1 per 9.33 hours), although aggressive interactions involving fights and chases were rare. Sugiyama et al (1965) at Dharwar and Ripley (1967) at Polonnaruwa, found that, like Kanha, encounters were daily events and both suggested that inter-troop relations were territorial. However, Vogel (1975,1977) disputed this conclusion. After a brief investigation of langurs at Bhimtal and Sariska he concluded that territoriality in langurs is 'highly questionable' but that inter-group conflicts function as 'defense of group integrity and social order'. Such an interpretation may be applicable to troop-band interactions. Indeed, as pointed out by Hrdy (1977b), Vogel's encounters were of this type and therefore his data are not comparable with studies of inter-troop interactions.

The most detailed published study of langur intergroup relations is found in Hrdy (1977b), who like Ripley (1967), was surprised to find troops seeking out other troops even though endowed with excellent spacing devices (whooping, displays, visual scanning). Encounters with both types of group were frequent and similarly to Kanha 76% of band contacts occurred in the troop core area whilst troop encounters occurred at the periphery. As was the case in Kanha troop-troop encounters were stylized. Physical contact was rare, despite a high frequency of chases and it was never seen to result in injury. Adult males generally initiated encounters but females 'played major offensive roles' on 58 % of occasions. In contrast, troop-band contacts were escalated fights, more frequently resulting in injury and were largely male affairs.

The Himalayan fieldwork suggests that encounters are considerably less frequent there than in peninsular populations. Bishop (1979) suggests that with the reduced frequency of contagious 'whooping', in the Himalayas, visual scanning by adult males is used to avoid other troops. Vogel (1971) proposed that 'whoop concerts' are rarer in the mountains because echoing would confuse determination of the location of the sender. Orcha and Kanha are both very hilly and yet whoops are given prolifically and Bishop (1979) could locate whoop callers, despite the Himalayan topography. Ripley (1967) suggested that there is a relationship between density and encounter frequency. The compression of ranges at high density into a contiguous pattern may exacerbate conflict between troops. Perhaps there is a gradation, with inter-troop avoidance more important, through visual and acoustic location, at low density, when range size is large, but site-dependent territorial conflict at high density, when ranges are small and site defence becomes possible (Mitani & Rodman 1979), and a necessity for maintaining exclusive access to food and/or mates.

Among other colobines, Presbytis johnii (Poirier 1968) and Presbytis senex (Rudran 1973, Hladik 1976) were concluded to be territorial. Curtin (1980) compared the social organisation of sympatric P.obscura and P.melalophos in Malaya, recording few encounters and little range overlap in both species. Perhaps some form of visual and acoustic avoidance was responsible for the overdispersed pattern of ranges.

Of the African colobines Oates (1977b) found that a black and white colobus troop had daily encounters with 74 % range troop overlap. Oates recorded the spatial distribution of outcomes and found evidence of site-dependent inter-troop conflict. Struhsaker (1975) found that red colobus encounters, 36 % of which were aggressive, occurred on 59 % of observation days. Three troops used a patch of forest, with high range overlap, to the near exclusion of conspecifics, but dominance relations between these troops were independent of location. This appears to be the only colobine with such an arrangement, red colobus being unusual in many respects (Hrdy 1977b).

I gained the impression that at some locations actual physical landmarks were being used as troop boundaries. The sunken nullah in Q 20/19 appeared to be respected by "C" and "L" as a division and a gap between boulders in 9/14 appeared to be used by "C" and "A" as a spatial reference. Interestingly, after the replacement of AM^{23} by AM^{30}, which had not been seen in the area before, the spatial relationship between "A" and "C" did not change; perhaps range boundary information is preserved in the matriline. Stability of spatial relationships over a decade is indicated by the "A"-"C" boundary in this study being coincident with the "B"-"A" boundary of Nagel & Lohri (1973).

The tendency for langur troop-band contacts to occur in the morning is perhaps the result of extra-troop males using the 'whooping chorus' to locate troops, giving maximum daylight hours in which to monitor, consort or attempt invasions. The chorus may also allow troops to put spatial fixes on adjacent groups and hence avoid contact whilst replenishing the nocturnal fast. The increased frequency of encounters towards dusk may reflect troops actively seeking out other troops after feeding. It may also arise by chance from independent ranging patterns after the initial mutual fixing of location.

However, why are troop-troop and troop-band relationships different ? The dichotomy may reflect differences in the costs and benefits to the opponents in conflict (Brown 1964,Hrdy 1977b,Harrison 1983b). If "C" was territorial with respect to other troops, and the evidence is inconclusive, whatwere they defending ? Territoriality may have a variety of functions, with the defence of food supplies and access to mates the most likely advantages for langurs. For troop-troop interactions the observations support the importance of the former function:

a/ Some encounters appeared to involve conflict over particular, highly selected, tree species occurring in the overlap zone. In July 1981 "C" for the only time made excursions towards the west (Q 5/15 region) into an area which had been exclusively occupied by "A" since February. Also in July, "A" and "C" encounters peaked in frequency (see Fig 8.22) with "A" winning 78 % of those with a recorded outcome. This expansion in ranging towards the west and increase in "C" losses appeared to be related to foraging, in that the 5/15 area contained the highest density of Saccopetalum in the grid (see Fig 5.8) on whose fruits "C" spent 21.1 % of feeding time in June and 4.3 % in July with a high selection ratio (see Chapter 9). "C" foraged extensively on this species at this season at Kuloo chattan, but the bushes showed pronounced signs of depletion. It would therefore seem likely that "C" expanded its range into an area used intensively and otherwise exclusively by "A", to poach fruits from a clump of Saccopetalum, when the supply had been depleted in its own area. Indeed, on these forays to the west, "C" fed largely on Saccopetalum fruits.

The encounters between "C" and "N" from December 1981 until January 1982 similarly appeared to be related to a pair of Pterocarpus trees in the overlap zone at Q 7/21. The mature leaves of the tree constituted 24-37 % of the diet in these months with a high selection ratio (see Chapter 9) and the trees at the chattan may have been depleted of leaves. These circumstances may have led to "C"'s foraging in the periphery of its range, bringing it into conflict with "N".

b/ If the defence of food supplies was occurring, encounters would be predicted to be infrequent when major depletable food resources were abundant and distributed symmetrically between the ranges of the two opposing troops (Harrison 1983b). Opposing troops have low 'motivation' for conflict over such resources, as the benefits accruing from their exclusive occupation would be minimal. Therefore, if langurs were defending trees it would be expected that enounters would be less frequent when feeding on abundant, omnipresent items, such as mature leaves, than when feeding on more ephemeral, patchily distributed items, such as flowers. The hypothesis is supported by a strong negative correlation between the % of mature leaves in the monthly diet and encounter rate (r_s=-0.814, n=12, p<0.01). The preponderance of "C" wins close to Kuloo chattan suggest that the troop may be defending this patch of high food tree density and diversity which contained many highly selected tree species.

In unimale troop-troop interactions both adult males may run a high risk of injury from escalated violent aggression. Such injury might increase the probability of a takeover occurring, resulting in the curtailment of reproductive activity and the killing of progeny. Troop males have little to gain from range expansion if the harem females have sufficient resources for raising his offspring. A larger range may be harder to defend (Mitani & Rodman 1979) and the tree species-area curve (Chapter 5) suggests that a wider ranging pattern, in a 'sea' of sal forest would add few new species. The females have similar interests to the male in site defense and, with little risk of injury, they also participate. There is therefore a symmetry (Dawkins & Krebs 1978) between troops in terms of costs and benefits, resulting in ritualised, low intensity encounters.

Troop-band conflict did not appear to be related to food resources as bands were seldom seen to feed in "C"'s range. The observations described in Chapter 6 suggest that reproductive factors may be more important. There is considerable asymmetry between the groups in terms of the potential cost and benefits of aggressive encounters. The troop male has access to a harem of breeding females, whilst the band males are the 'have nots' in terms of mating opportunity (apart from possibly taking advantage of adulterous solicitations). The troop male has nothing to gain from conflict with a band and the cost of losing will be high if takeover and infanticide result. In contrast, the band males have a lot to gain, but incur an increased risk of injury which might curtail reproductive success. Hrdy (1977b) found at Abu that 81 % of adult males and 33 % of adult females showed signs of injury. An injury to a male is potentially a much greater calamity to reproductive success than to a female, which can rear young successfully with a disability which might preclude a male from mating. In Kanha serious injuries appeared to be far more frequent among band males than females, but no troop adult male showed signs of past trauma. It is therefore hypothesised that the more violent, intense and longer troop-band conflict results from this asymmetry. The extra-troop males, with a numerical advantage, have much potential reproductive advantage to gain by entering the centre of the troop range, despite the remonstrations of the largely ineffectual troop male. If this interpretation is correct it may explain the difference in spatial outcome of encounters: trees, being sedentary, can be defended by site-dependent conflict, whilst the more mobile females cannot. Troop females, despite having much to lose, their current reproductive investment, as a result of a successful band invasion do not participate, probably because they would be ineffectual in countering the males. It is possible that they adopt a more subtle approach in the form of adulterous solicitations (see Chapter 6).

In conclusion, the study produced evidence that the relationships between troops and between troops and bands were different. The dichotomy can be interpreted in terms of the costs and benefits of conflict. Troops show evidence of site-dependent territorial defence of food supplies by ritualised, relatively unemphatic behaviour, as both antagonists have symmetrical costs and benefits: both troop males have food and matings. In contrast, bands invade the centre of the troop's range, resulting in violent conflict, with on occasions infanticide and takeover, as the opposing langurs have asymmetrical costs and benefit; troop males have matings whilst band males do not.

8.7 RANGING PATTERNS AND INTER-GROUP RELATIONSHIPS:SUMMARY.

1/ "C" troop occupied 298 quadrats, or 74.5 ha, during twelve months of observations. The intensity of use of each quadrat was estimated from 7 full days per month in which the quadrats occupied by the troop were recorded during scans at 30 minute intervals. Comparison of vegetation composition and the frequency of range use suggested that langurs occupied mixed forest more and meadow less than expected on the basis of abundance of habitats.

2/ "C" range utilization was concentrated at the centre of the grid, at Kuloo chattan, and about half of the annual range was occupied each month. Indices of diversity, clumping and range overlap were calculated for each month. The April range pattern was the least similar to other months, perhaps owing to infant-bearing females avoiding an infanticide-prone band. Troop dispersion showed little variation, suggesting that differences in range use were a consequence of distance moved and not troop spread.

3/ The centre of "C" range was used exclusively by it with respect to other troops but not in relation to bands. Four adjacent troops overlapped by 50.7 % with "C"'s annual range and were observed within it on 63.8 % of follows. Bands overlapped by 44.6 % and were present within it on 29 % of follows.

4/ Intra-specific variation in troop range size suggests that Himalayan troops have larger ranges than those of the peninsula and that range size is small in high density populations. The large band ranges, encompassing a number of troops, are interpreted in terms of differences between troop and extra-troop male reproductive strategies.

5/ Encounters, defined as the proximity of two or more groups less than 50 m apart, occurred with a frequency of 0.99/day (0.68/day for troops,0.26/

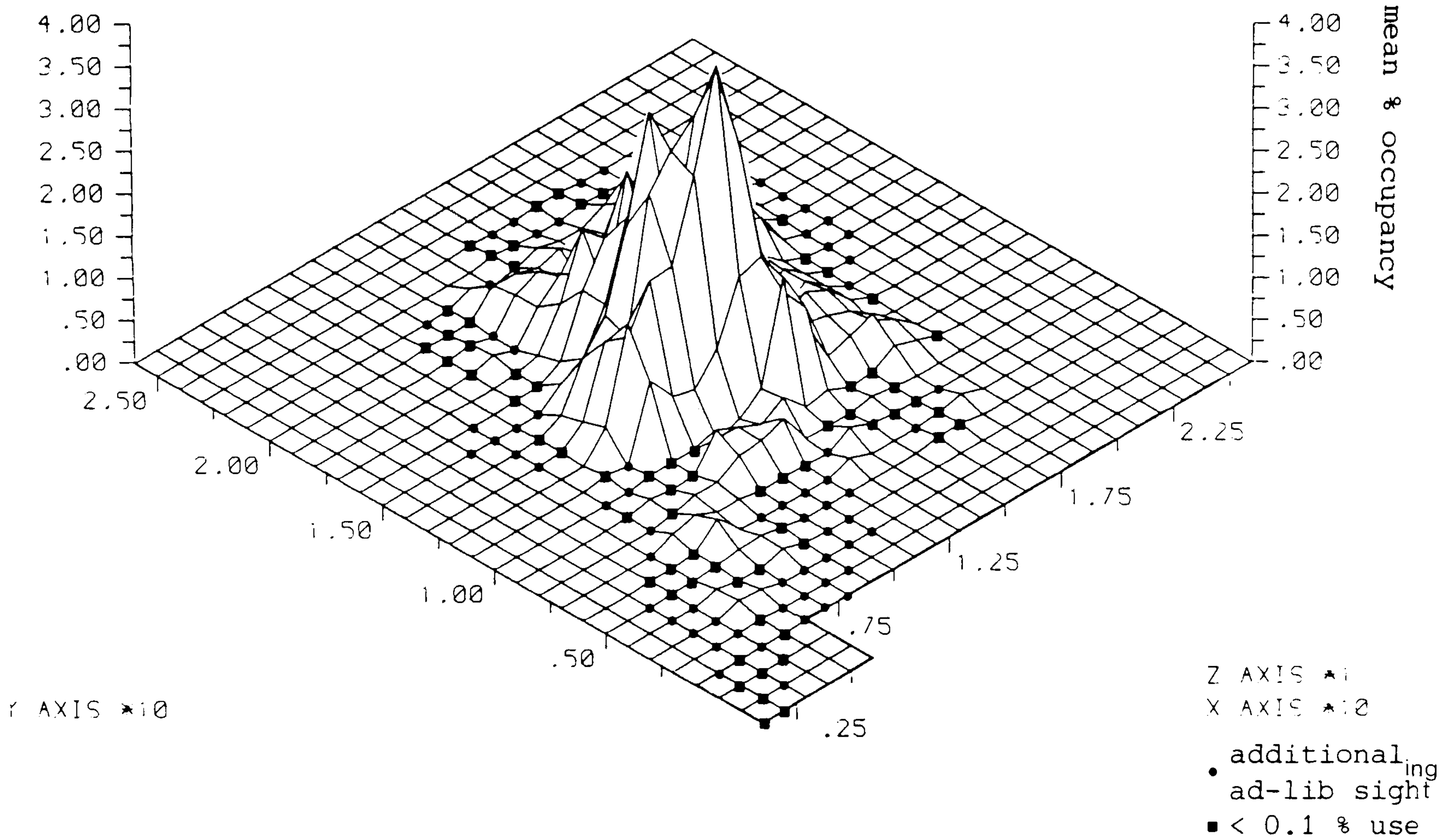
day for bands). Contacts were most frequent in the hot weather and early monsoon. Troop-troop encounters were most prevalent in the late afternoon and troop-band encounters during the morning. Mean encounter duration was 38.8 minutes, with band encounters tending to last longer than those between troops.

6/ Troop-troop encounters occurred mostly in the periphery of "C"'s range whereas band-troop contacts occurred in the range centre. The "C" adult male was involved in most encounters but females and immature participation was confined to troop-troop contacts.

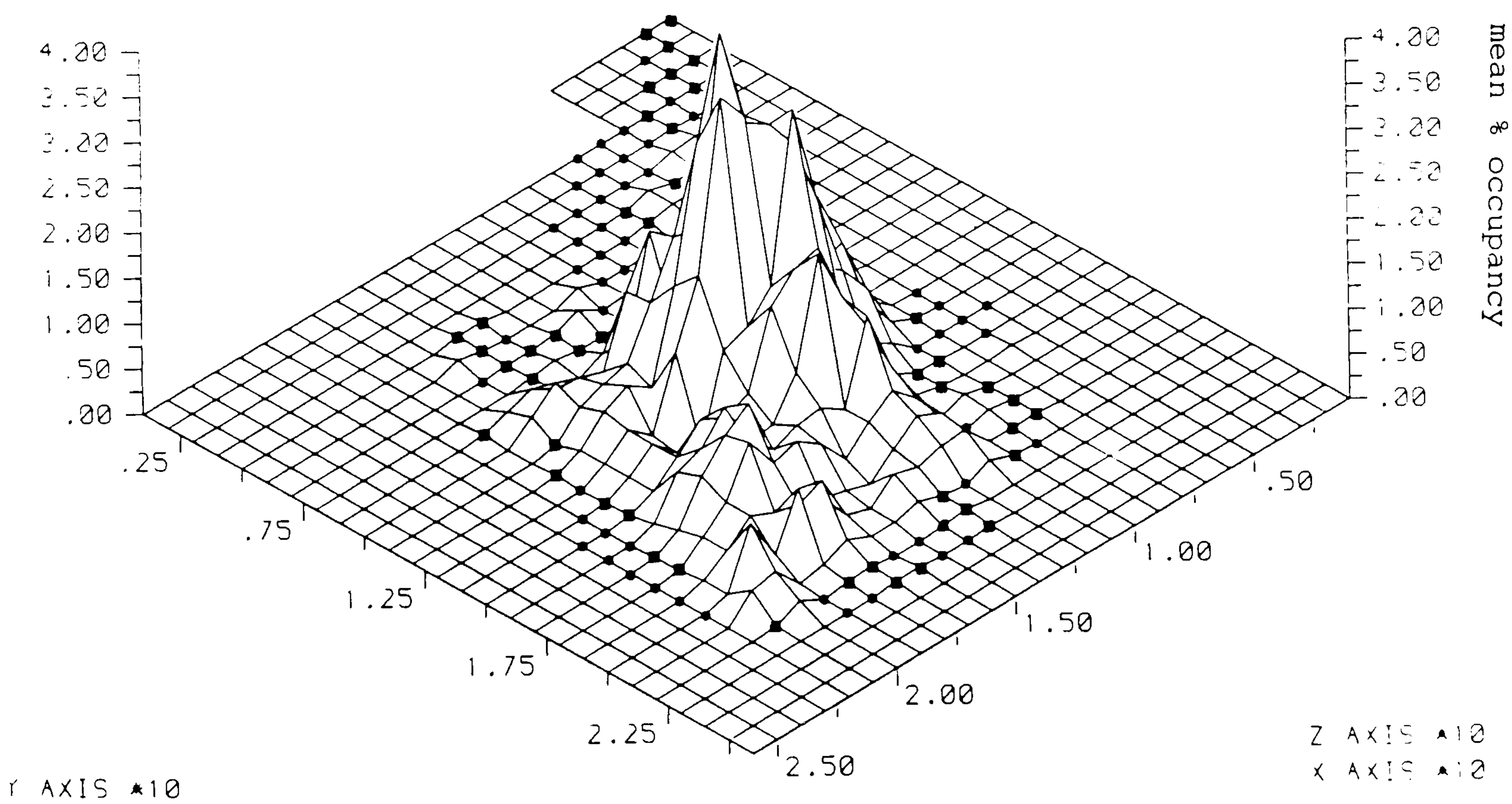
7/ Aggressive behaviour occurred in all but 6.25 % of encounters, which involved inter-troop immature play. Circumstantial evidence suggested that physical landmarks were used as cues for sections of troop boundaries, and that some encounters arose as a result of conflict over two highly selected tree species occurring at the periphery of "C"'s range.

8/ The group initiating the encounter tended to win and the terminator to lose in terms of supplantation. About a quarter of encounters were recorded as neutral and "C" won and lost with similar frequency. The spatial pattern of encounter outcomes suggested that the over-dispersed pattern of troop ranges may be maintained by a system of territorial site-dependent defence, of the central part of the range at Kuloo Chattan, and not site-independent avoidance. The dichotomy between bands and troops in terms of spatial distribution and age/sex class participation is interpreted in terms of the asymmetry in costs and benefits in contests between the two types of group. Troop-troop conflict is proposed to be associated with the defence of food resources and the escalated troop-band encounters with the defence of reproductive access and of progeny. The hypothesis that troop-troop encounter frequency is related to the abundance and symmetry of distribution of important food resources between the opponents' ranges is supported by the observation of a strong correlation between the proportion of mature leaves in the diet and encounter rate.

FIG 8.1 GINOSURF PLOTS SHOWING THE ANNUAL PATTERN OF RANGE USE FOR "C" TROOP. (Expressed as mean of monthly range use patterns, see FIG 5.4,MAP 6,7 for base map.

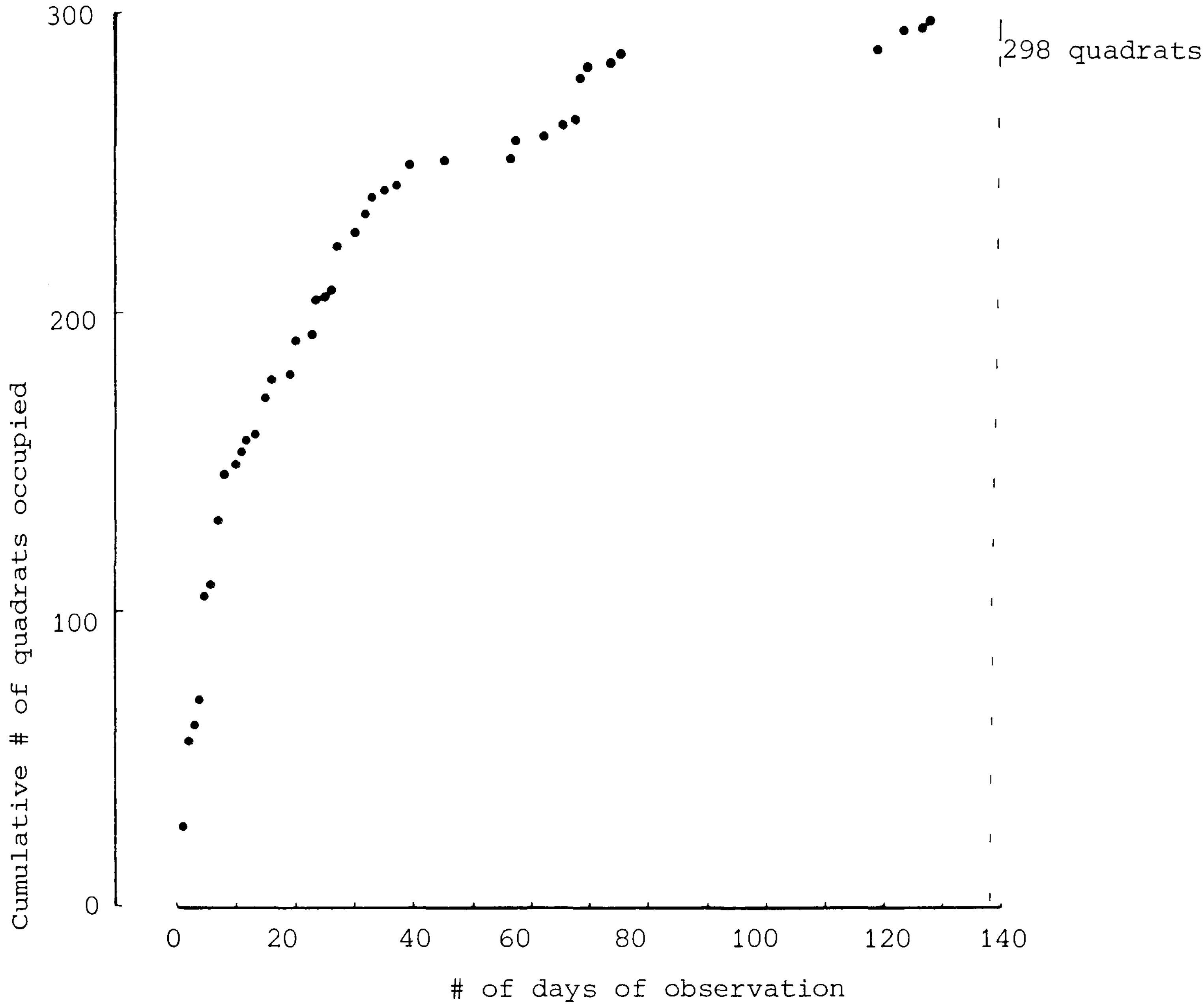


ANNUAL PATTERN (from SW)



ANNUAL PATTERN (from NE)

FIG 8.2 RATE OF INCREASE OF MEASURED RANGE SIZE WITH ACCUMULATION OF OBSERVATION TIME.



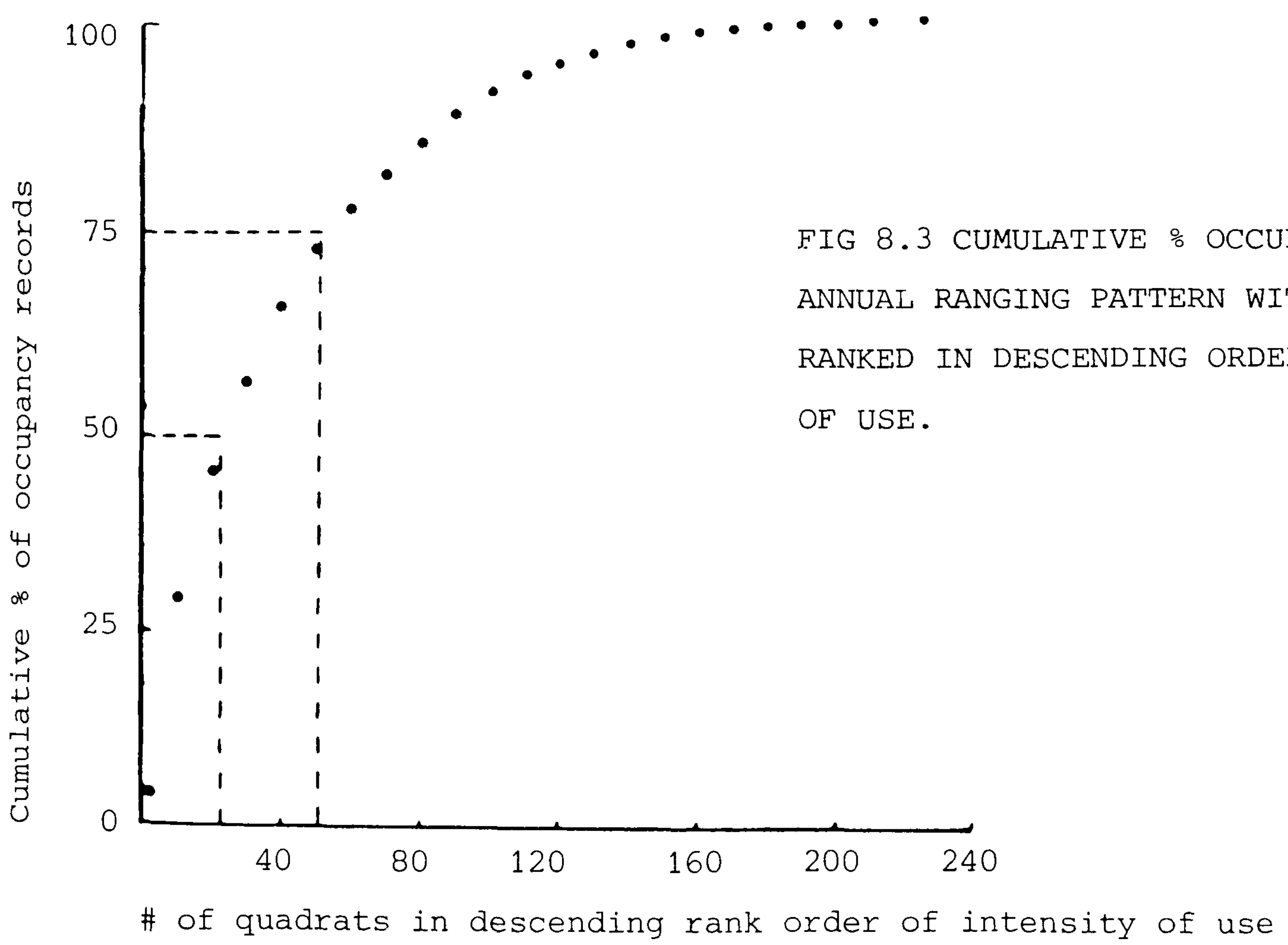


FIG 8.3 CUMULATIVE % OCCUPANCY FOR ANNUAL RANGING PATTERN WITH QUADRATS RANKED IN DESCENDING ORDER OF INTENSITY OF USE.

FIG 8.4 MONTHLY VARIATION IN HABITAT USE BY "C" TROOP.

a) Proportion of time troop occupied sal forest,mixed forest and meadow, monthly.

b) " " " " " " " " " " " , annual.

c) Proportion of grid occupied by " " " " " " .

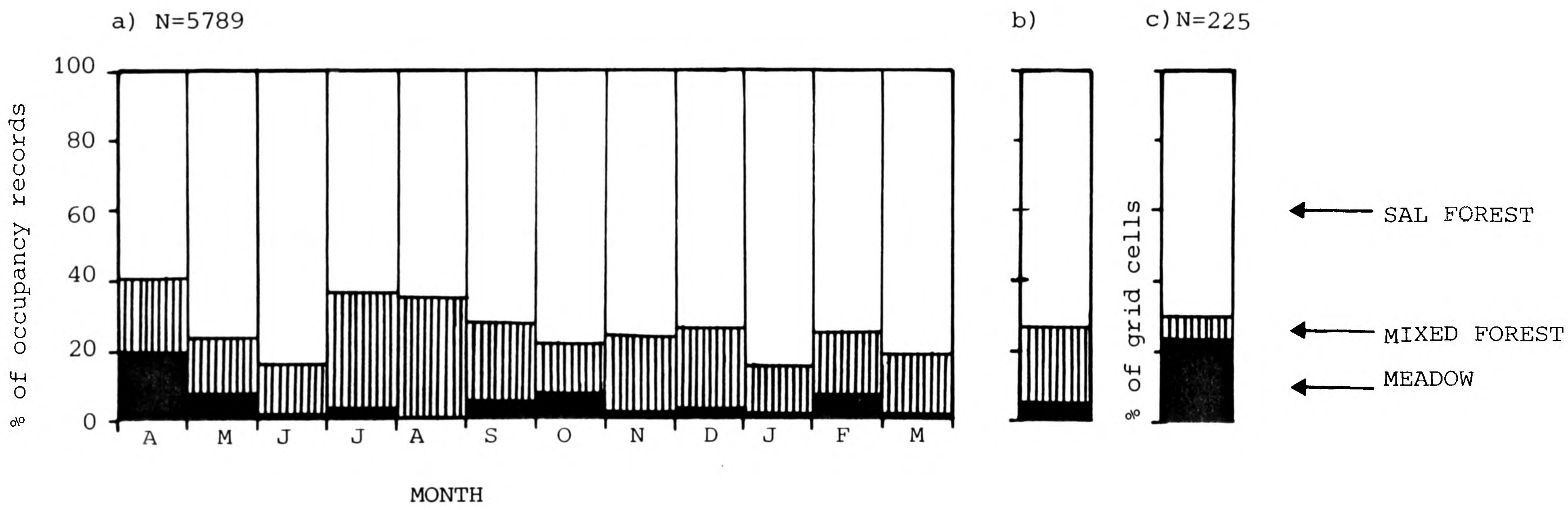
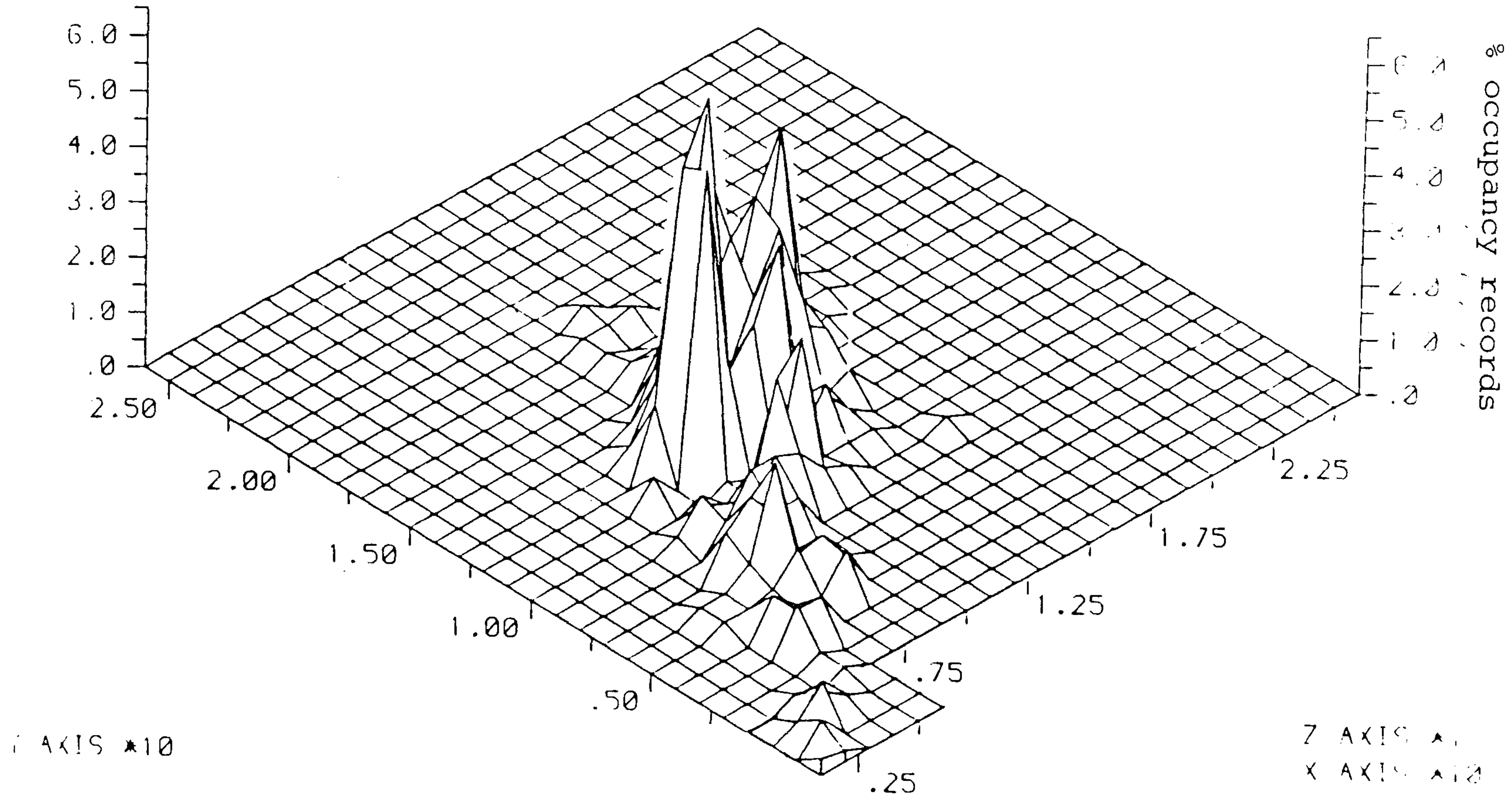
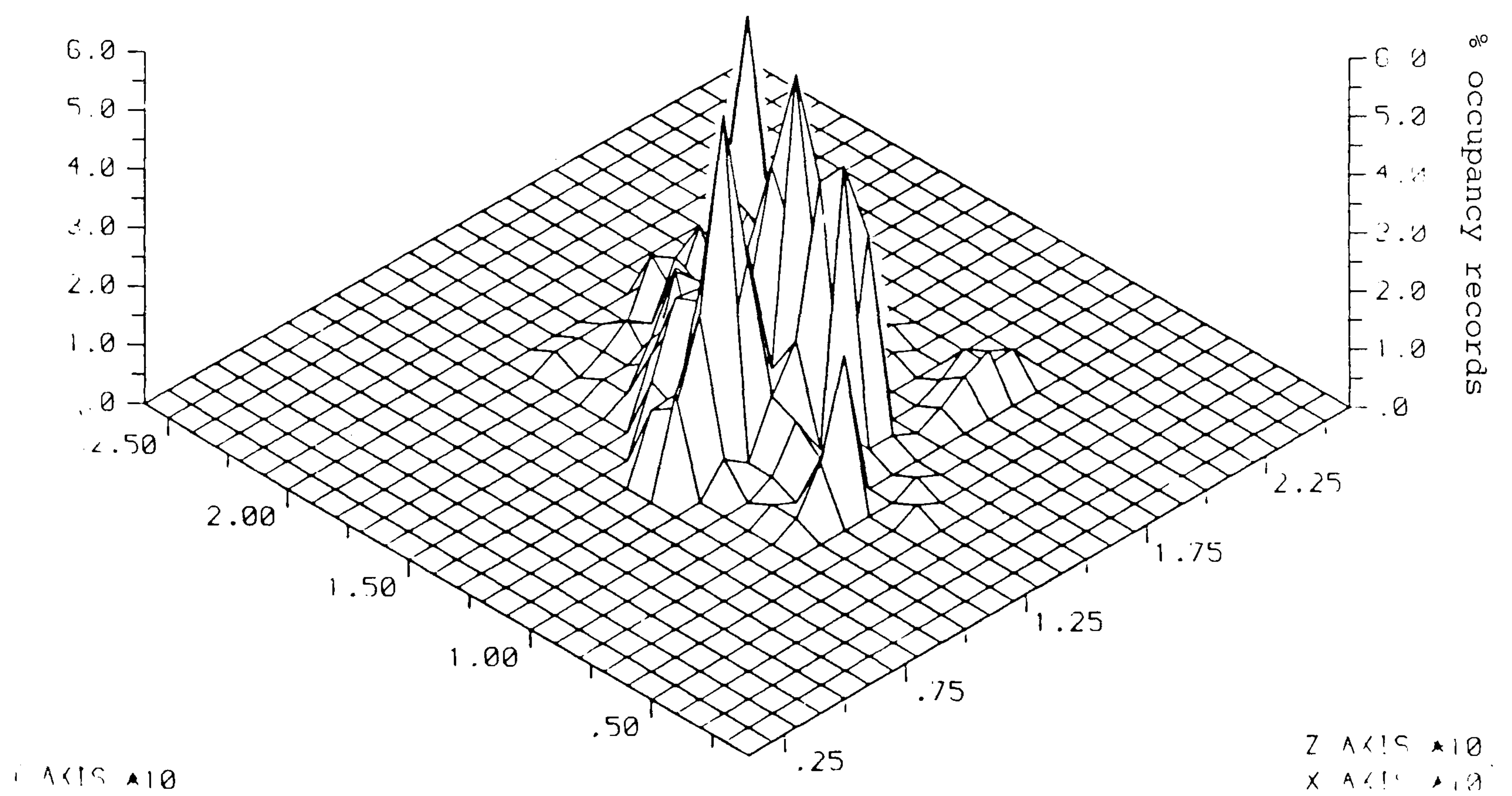


FIG 8.5 GINOSURF PLOTS OF "C" TROOP RANGE USE PATTERN.

(see FIG 5.4,MAP 6,7 for base map)



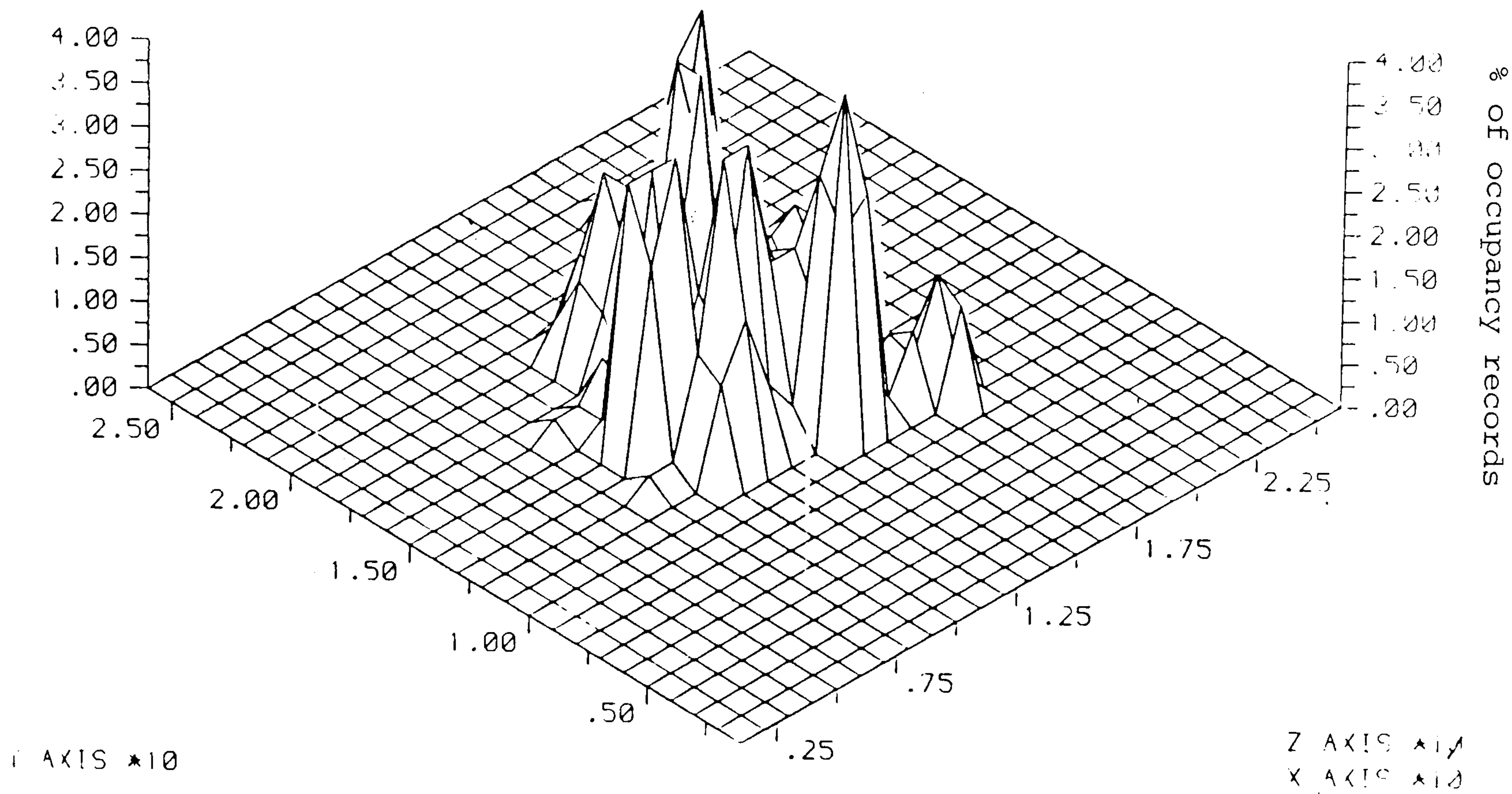
APRIL (N=608)



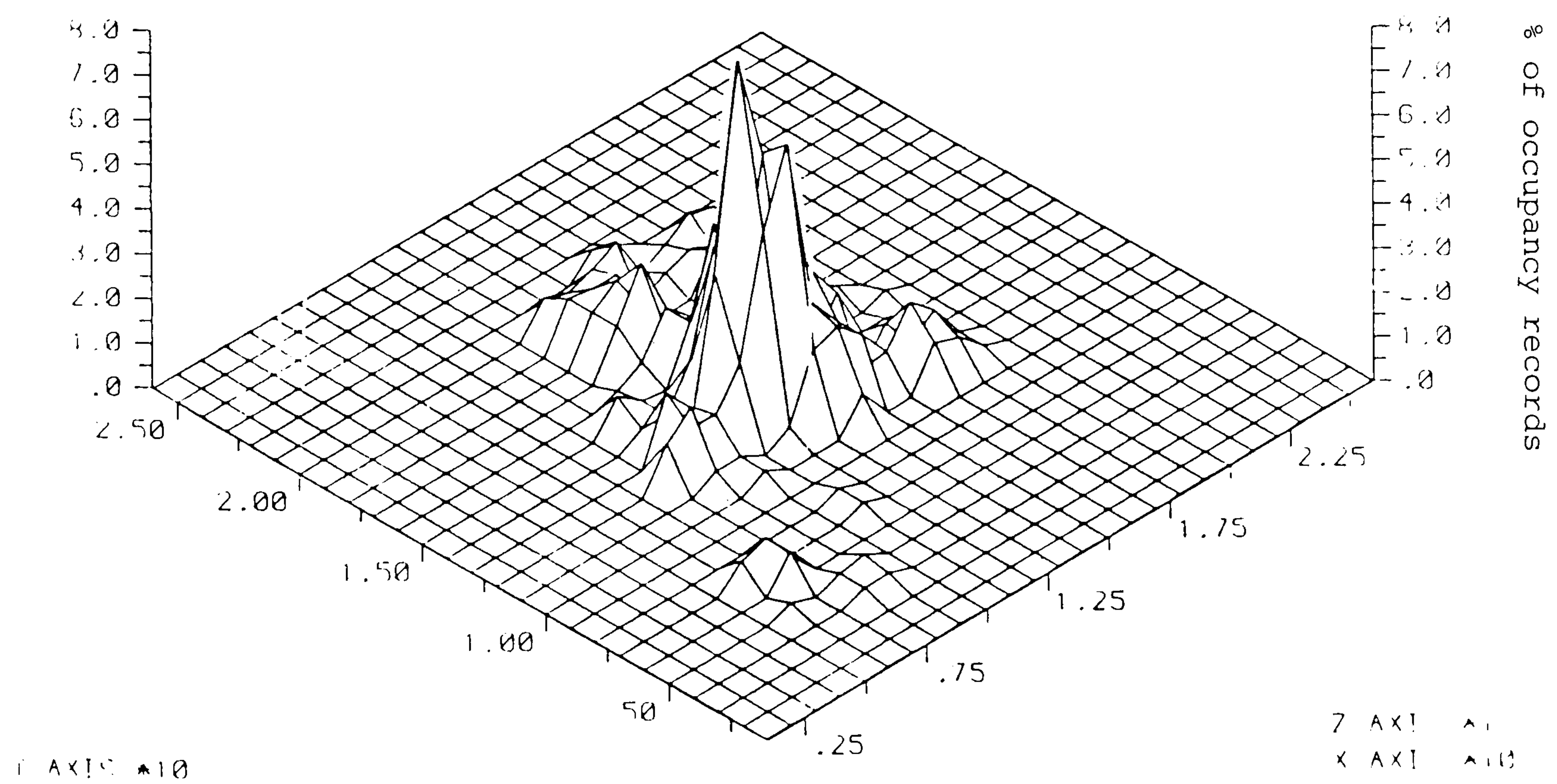
MAY (N=441)

FIG 8.6 GINOSURF PLOTS OF "C" TROOP RANGE USE PATTERN.

(see FIG 5.4,MAP 6,7 for base map)



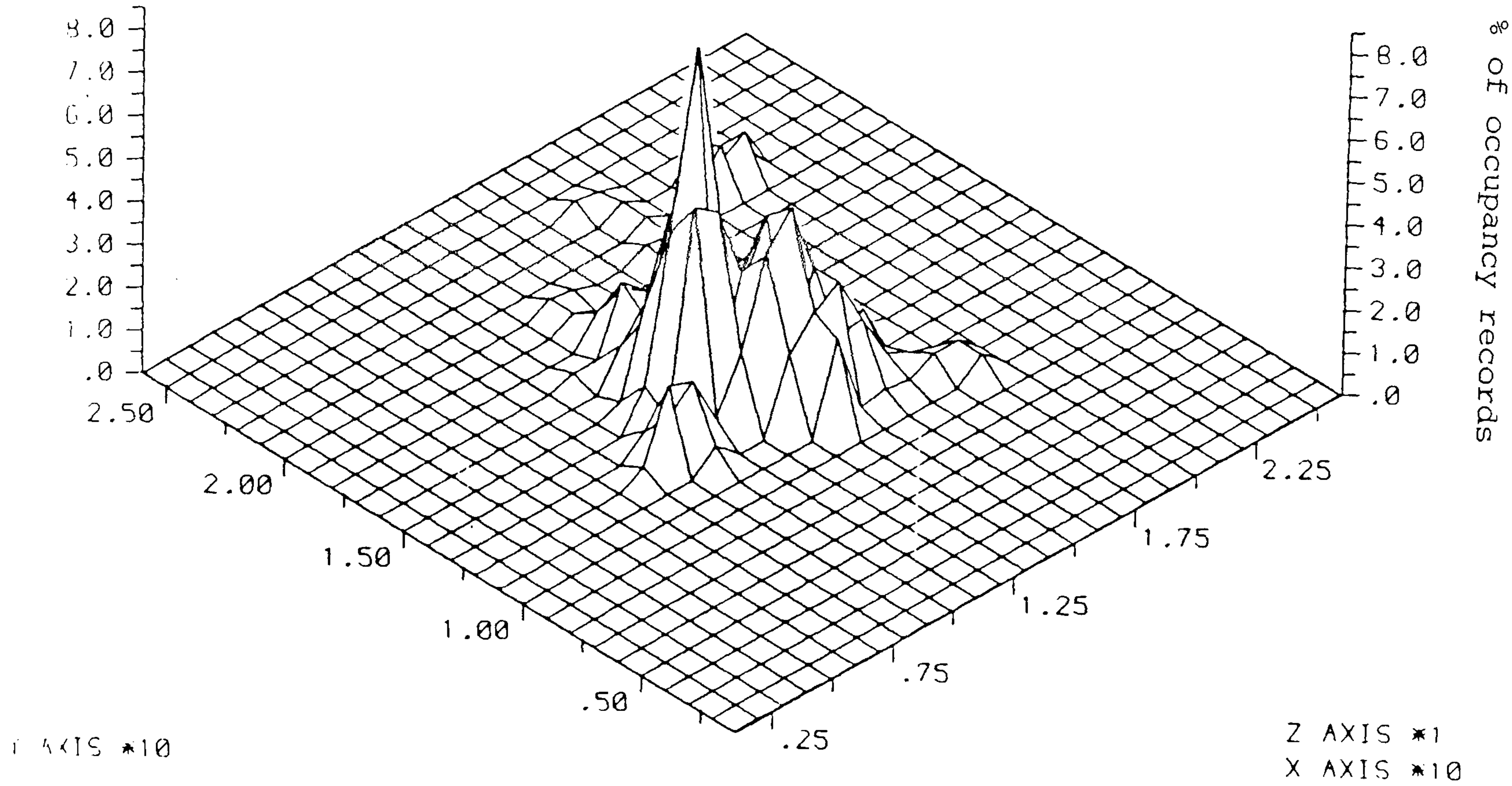
JUNE (N=523)



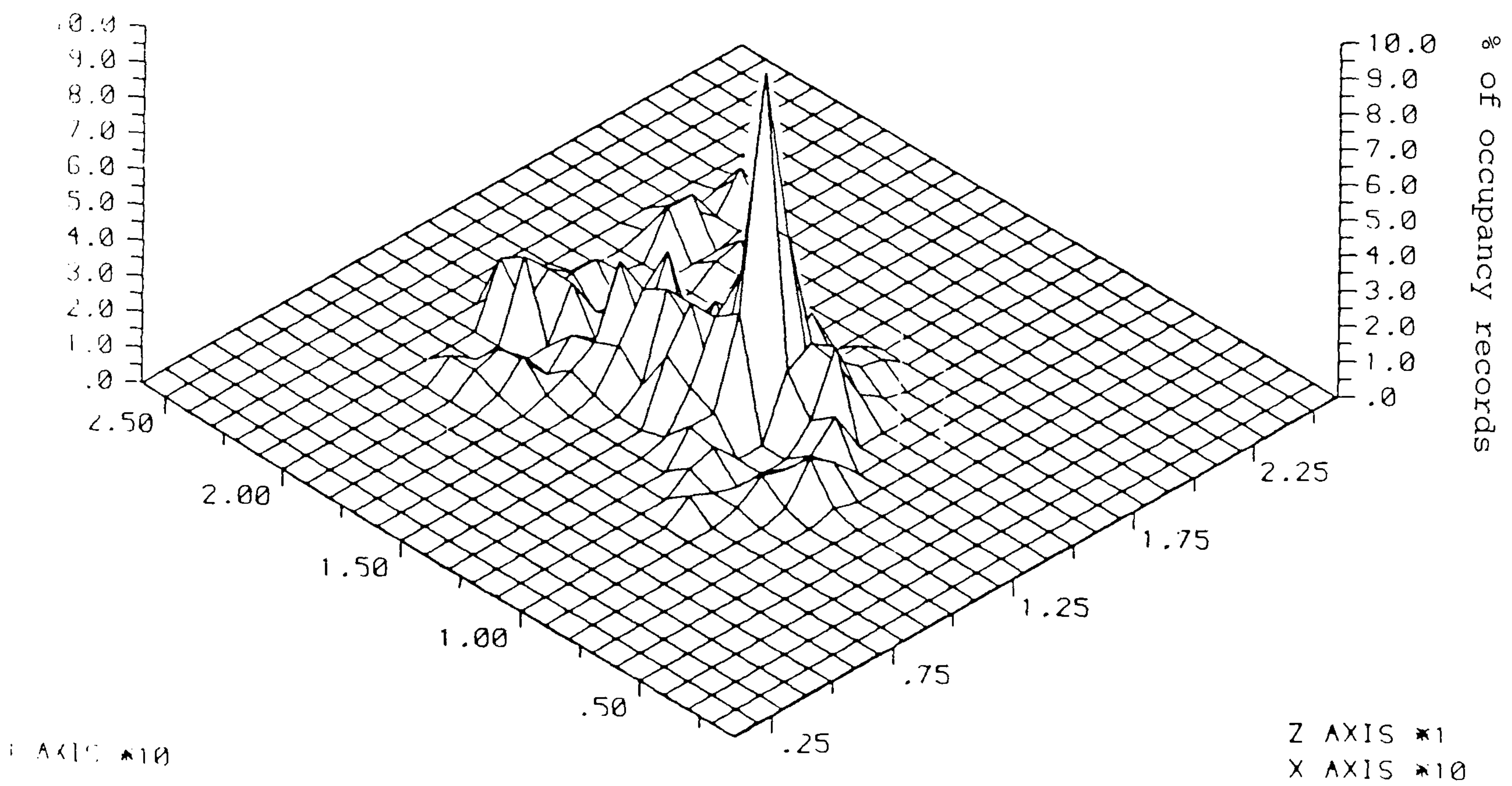
JULY (N=584)

FIG 8.7 GINOSURF PLOTS OF "C" TROOP RANGE USE PATTERNS.

(see FIG 5.4,MAP 6,7 for base map)



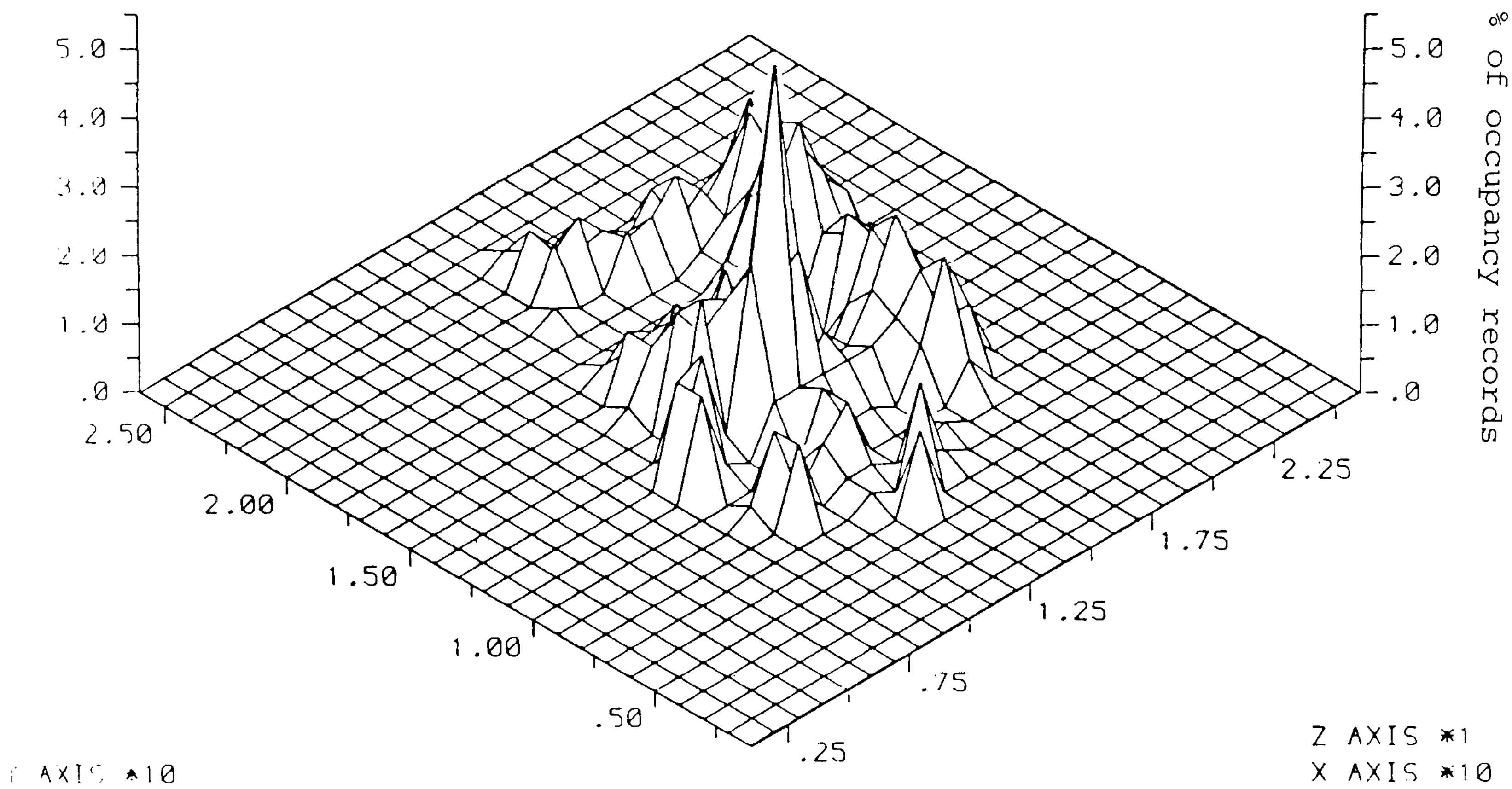
AUGUST (N=572)



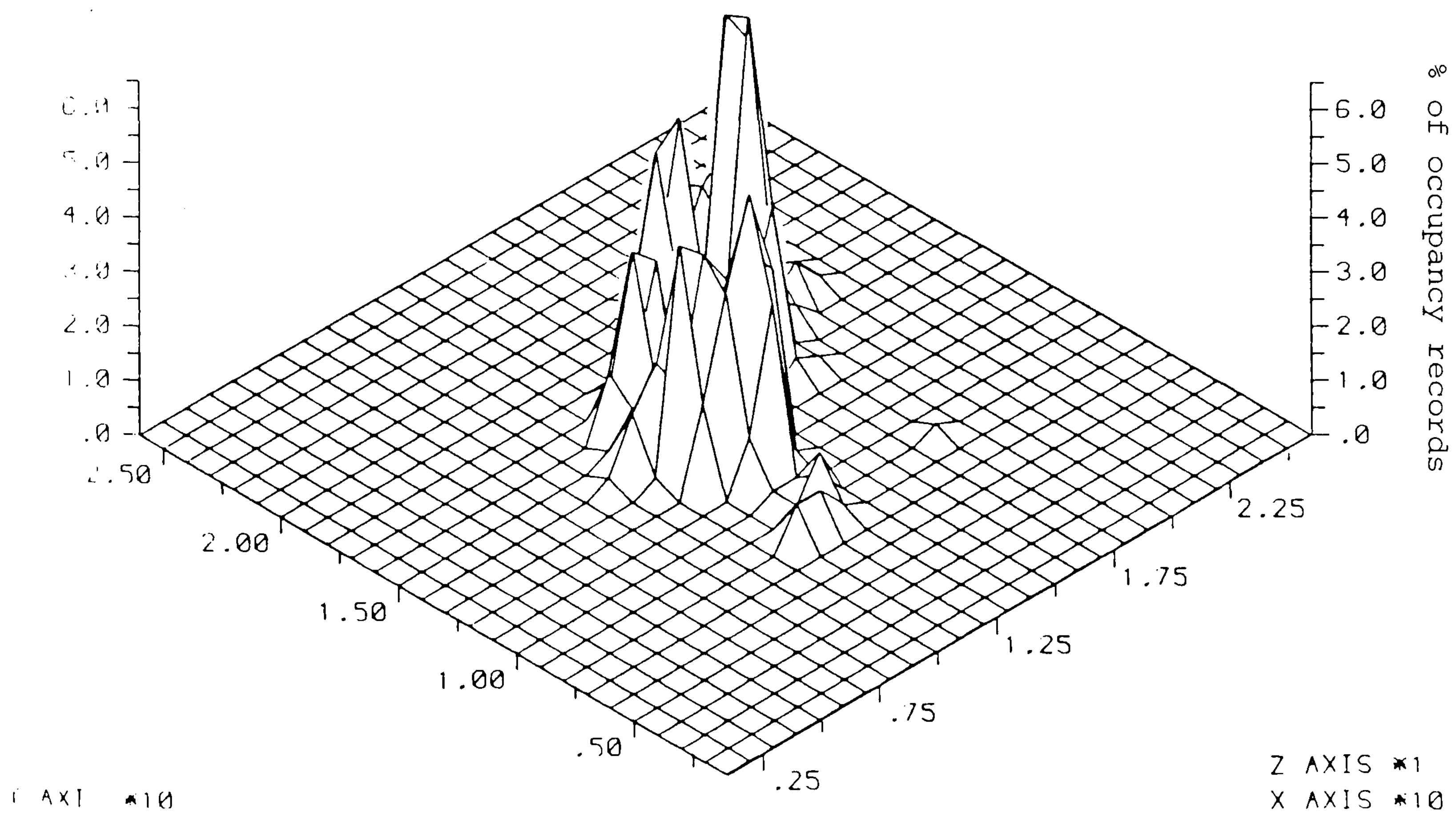
SEPTEMBER (N=423)

FIG 8.8 GINOSURF PLOTS OF "C" TROOP RANGE USE PATTERNS.

(see FIG 5.4,MAP 6,7 for base map)



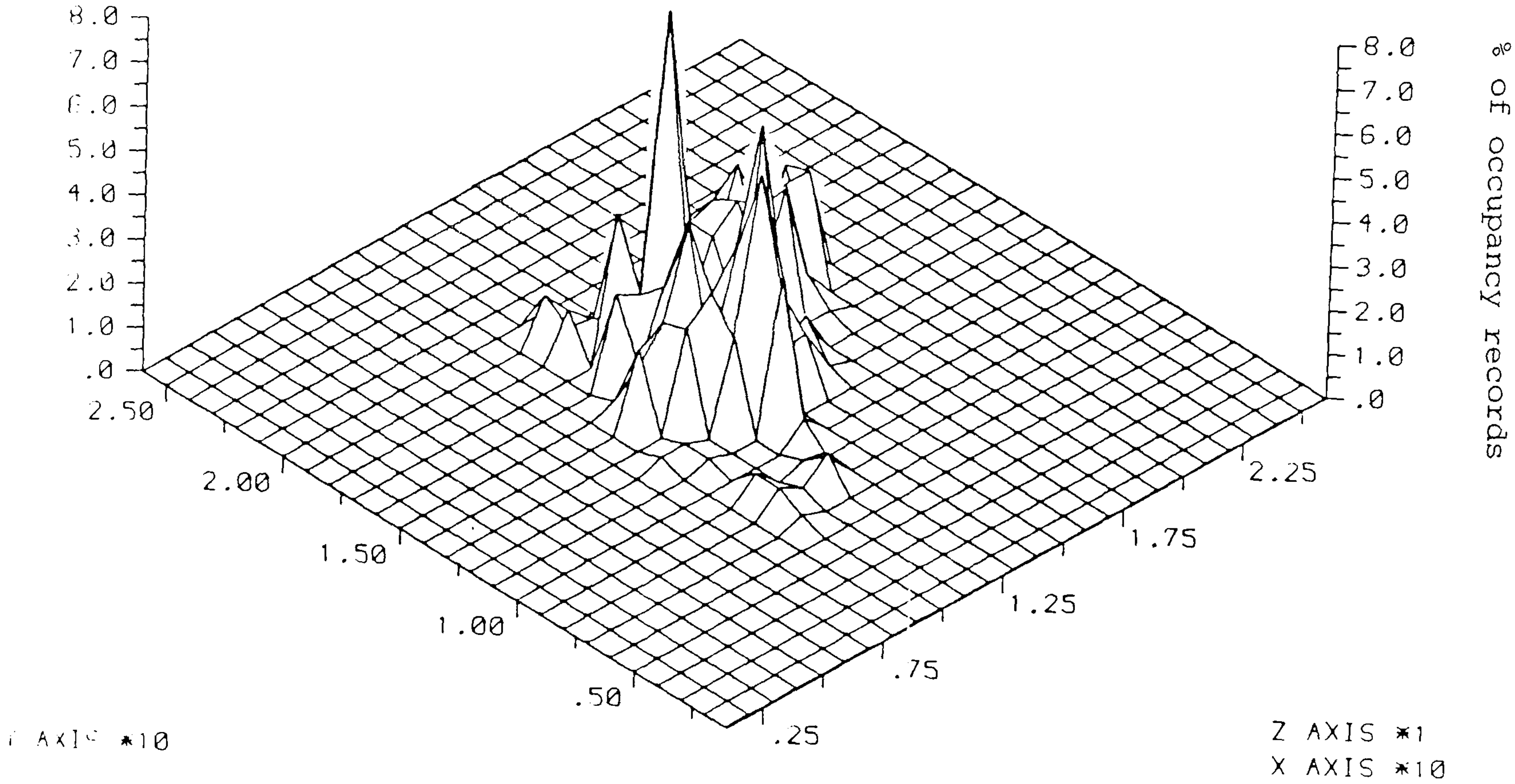
OCTOBER (N=444)



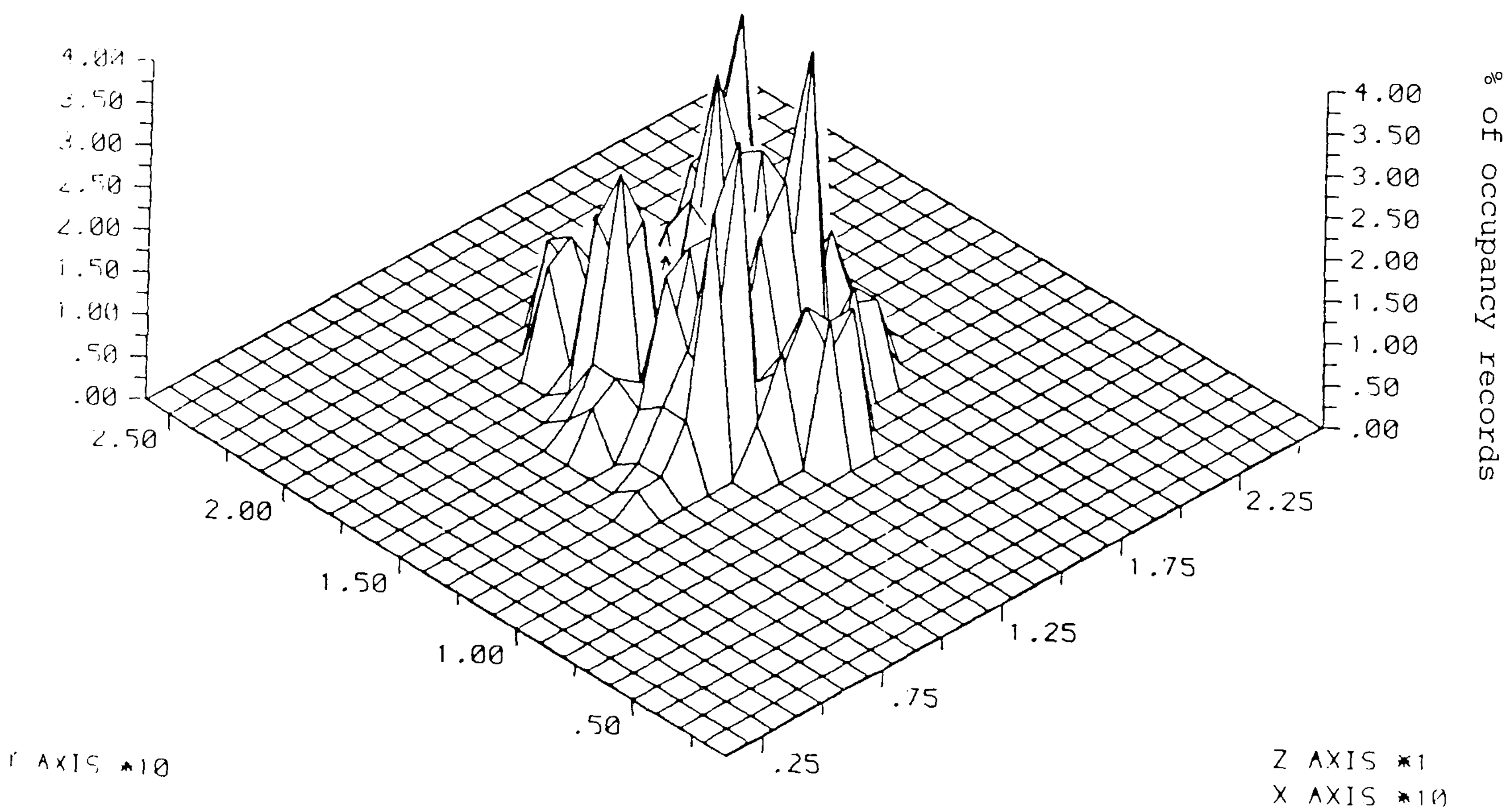
NOVEMBER (N=452)

FIG 8.9 GINOSURF PLOTS OF "C" TROOP RANGE USE PATTERNS.

(see FIG 5.4,MAP 6,7 for base map)



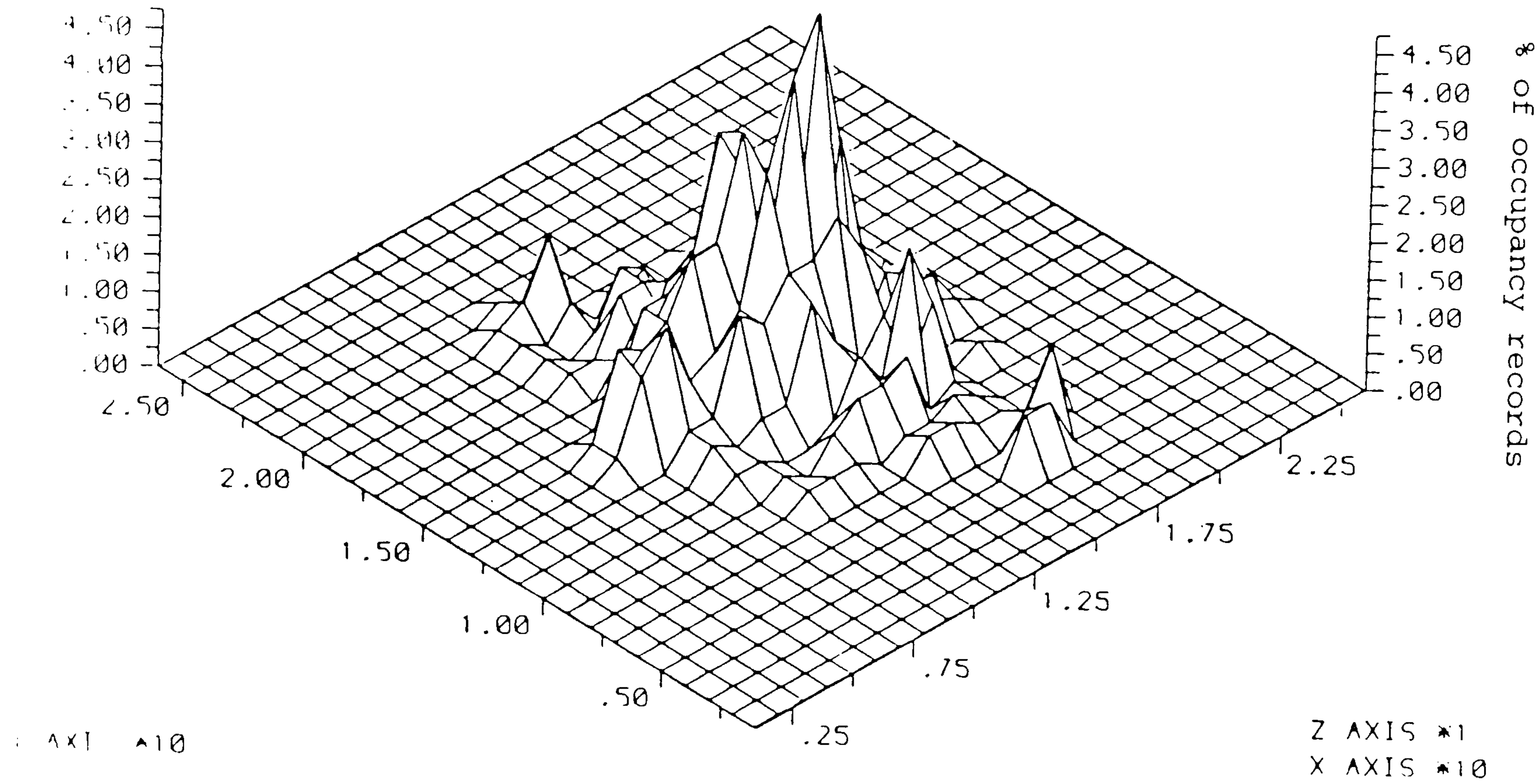
DECEMBER (N=410)



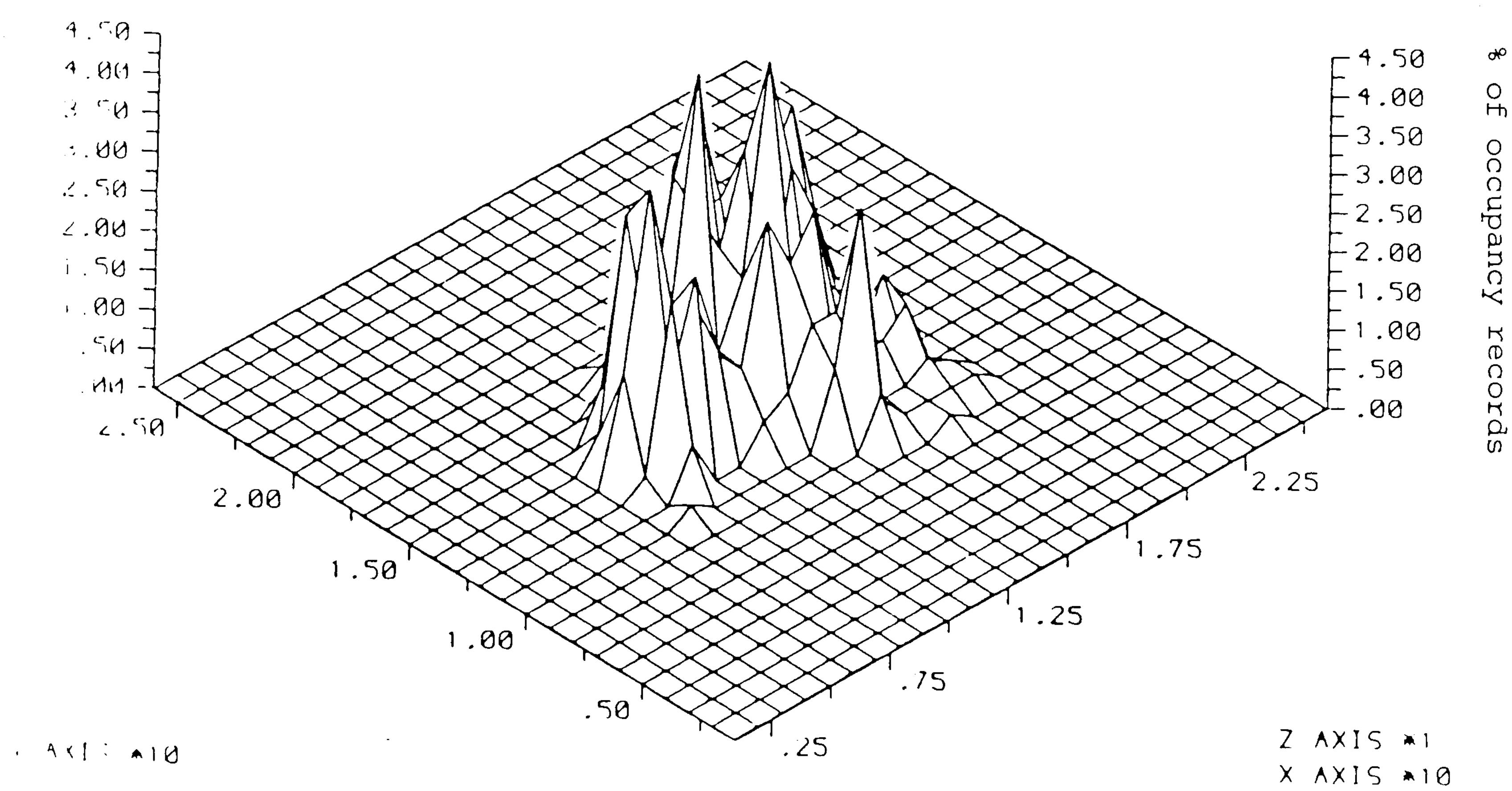
JANUARY (N=429)

FIG 8.10 GINOSURF PLOTS OF "C" TROOP RANGE USE PATTERNS.

(see FIG 5.4,MAP 6,7 for base map)



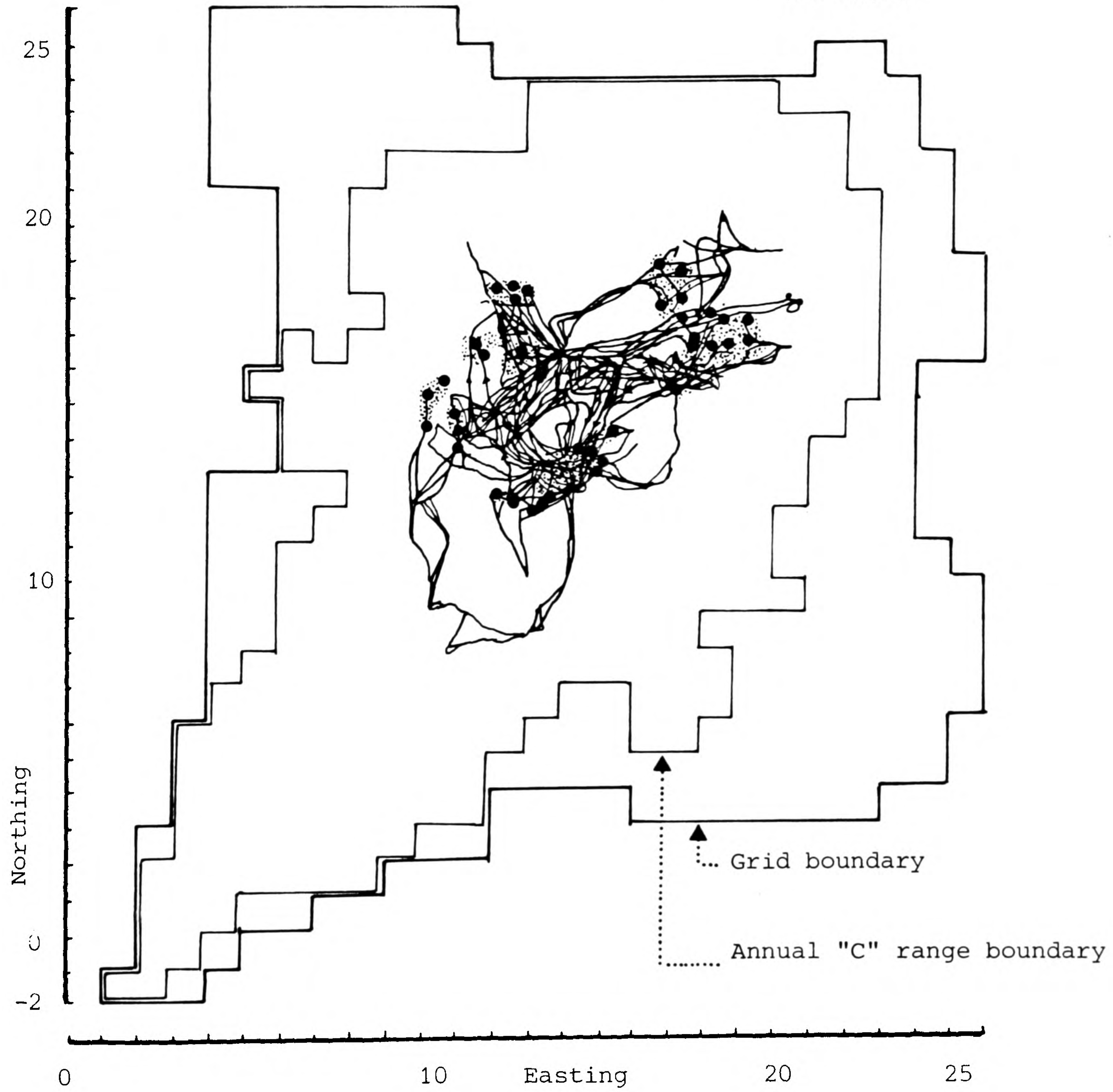
FEBRUARY (N=449)



MARCH (N=463)

FIG 8.11 EXAMPLE OF A "C" TROOP RANGE PATTERN : DECEMBER 1981.

(12 days)



●:sleeping site

0 200m

: extensive arboreal progressions.

route of centre of "C" troop

(See MAP 6,7 for physical and habitat features)

FIG 8.12 RATE OF INCREASE OF MEASURED RANGE SIZE WITH ACCUMULATION OF OBSERVATION TIME FOR EACH MONTH 1981-1982. "C" TROOP

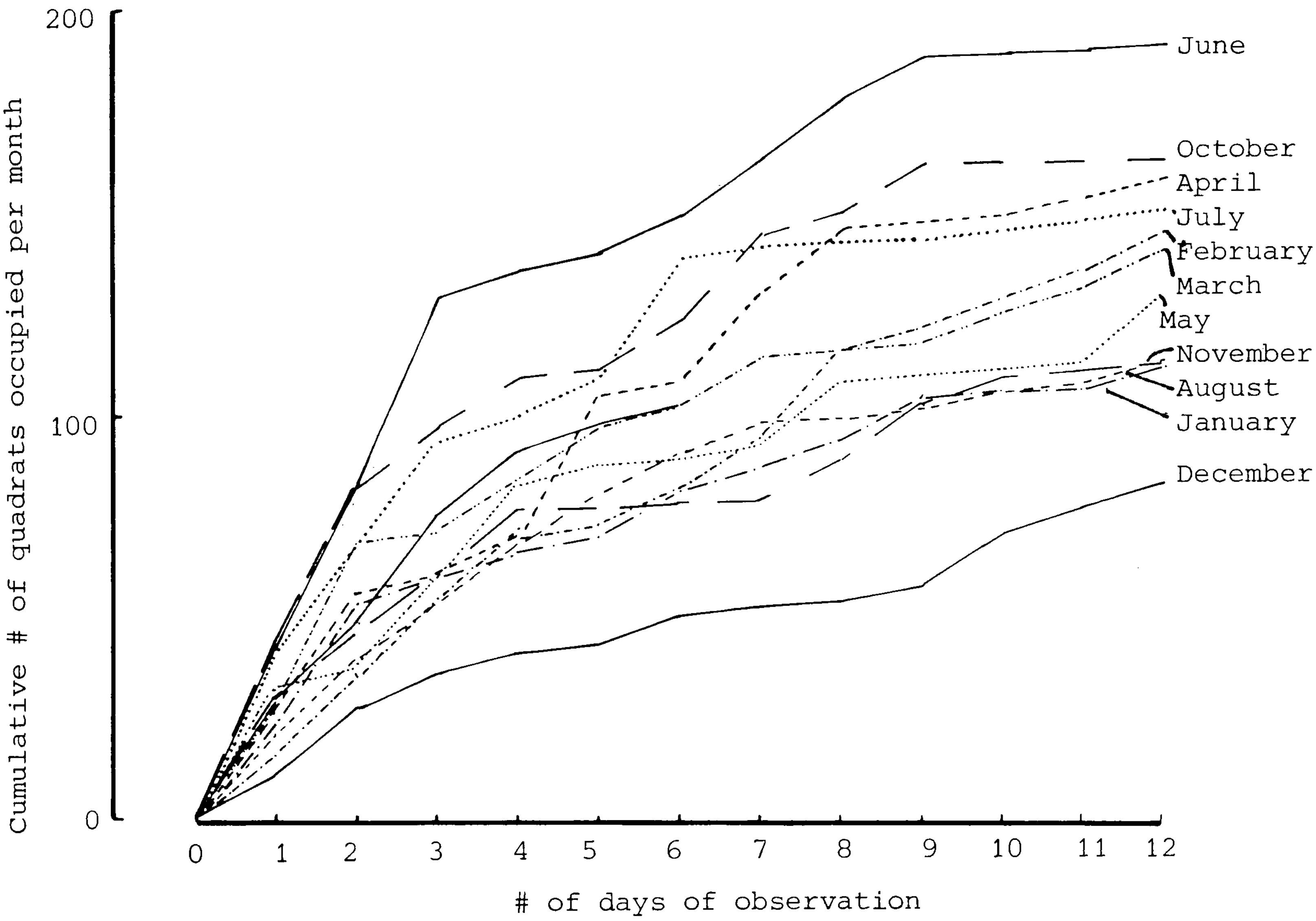


FIG 8.13 MONTHLY VARIATION IN RANGE SIZE,RANGING DIVERSITY (H') RANGE CLUMPING (RU) AND DISPERSION :"C" TROOP,1981-1982.

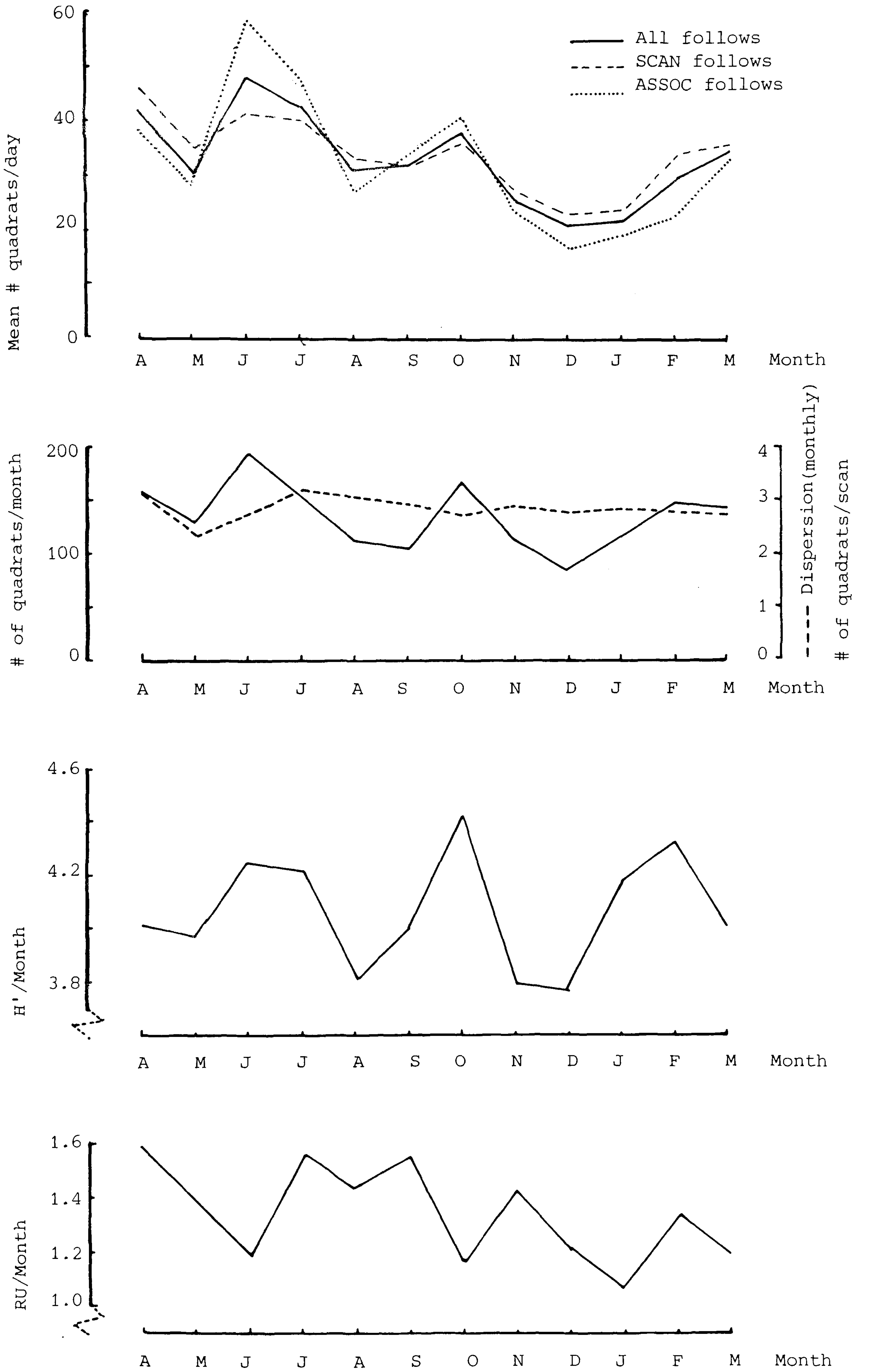


FIG 8.14 SINGLE LINKAGE DENDROGRAM OF MONTHLY RANGE OVERLAP.
(see text).

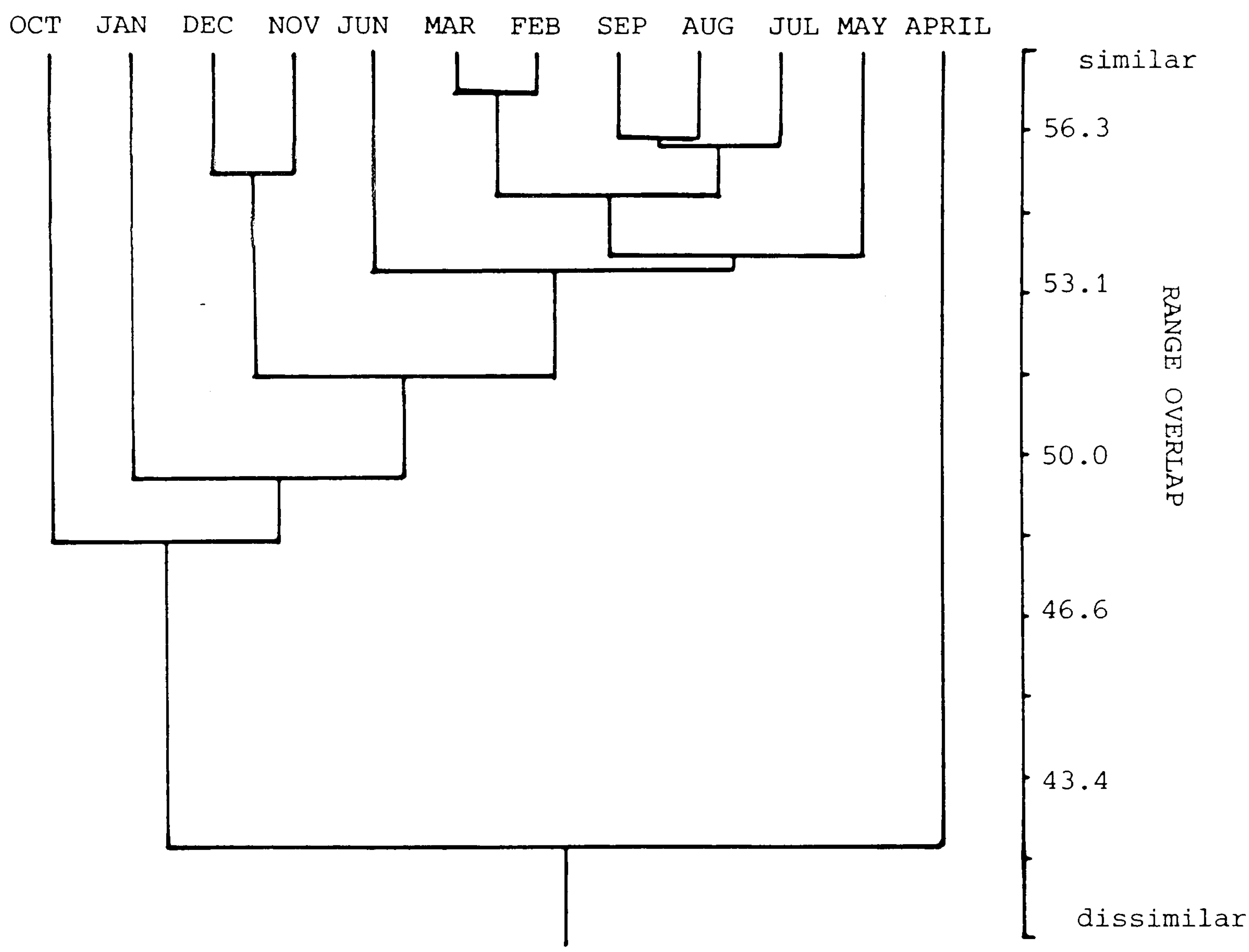
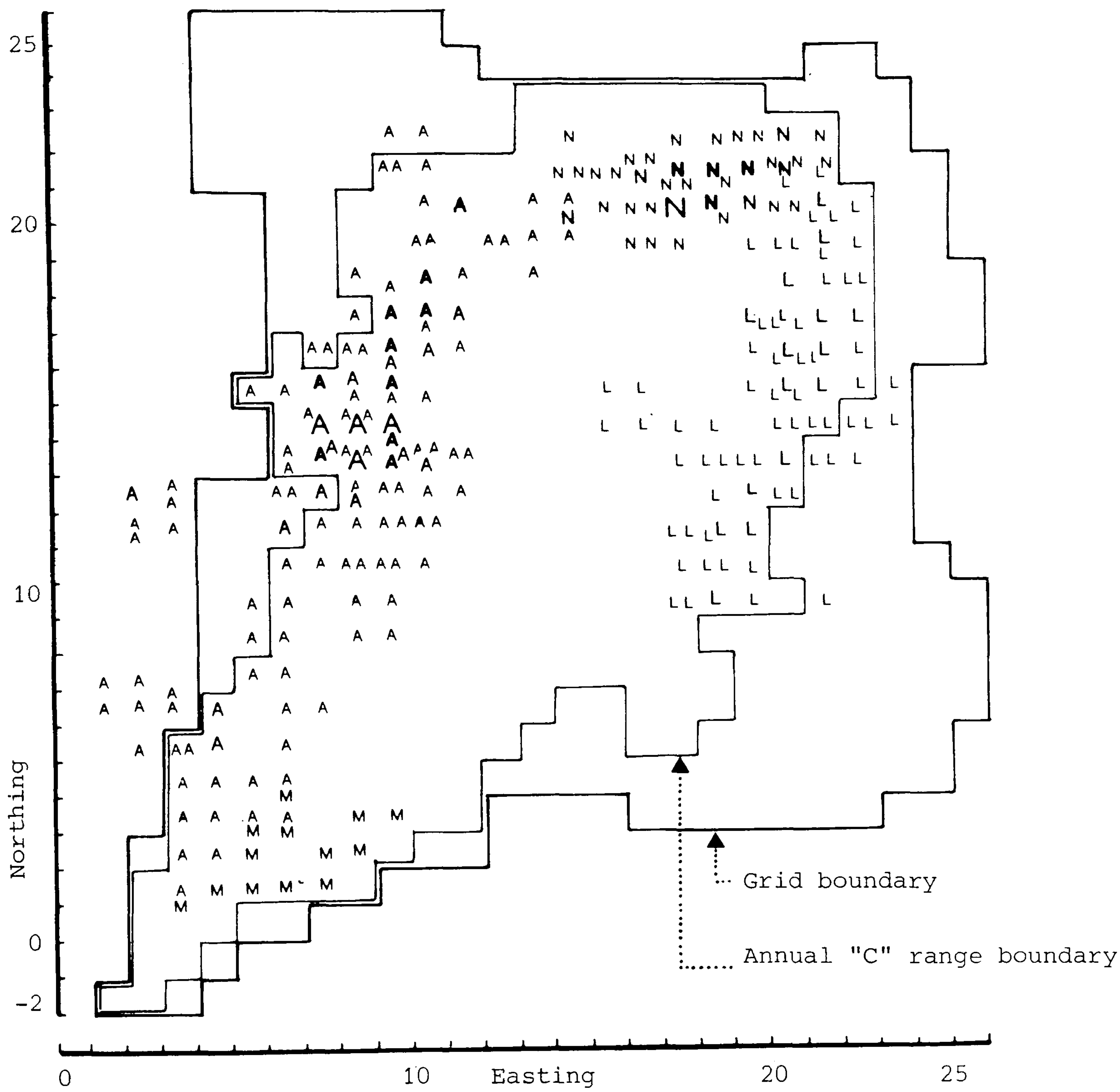


FIG 8.15 FREQUENCY WITH WHICH FOREIGN TROOPS OBSERVED IN "C" TROOP STUDY SITE,DURING FOLLOWS: APRIL 1981-MARCH 1982.

(See MAP 6,7 for physical and habitat features)



0 200m Symbol indicates troop identity i.e. A = "A" troop

Size of symbol indicates number of days troop observed in 138 days total

N 1 N 3 N 6 N 10

FIG 8.16 GINOSURF PLOT SHOWING ANNUAL PATTERN OF "C" TROOP RANGE USE. (same figure as FIG 8.1) for comparison with plot (below) of use of same area by other troops. April 1981- March 1982.

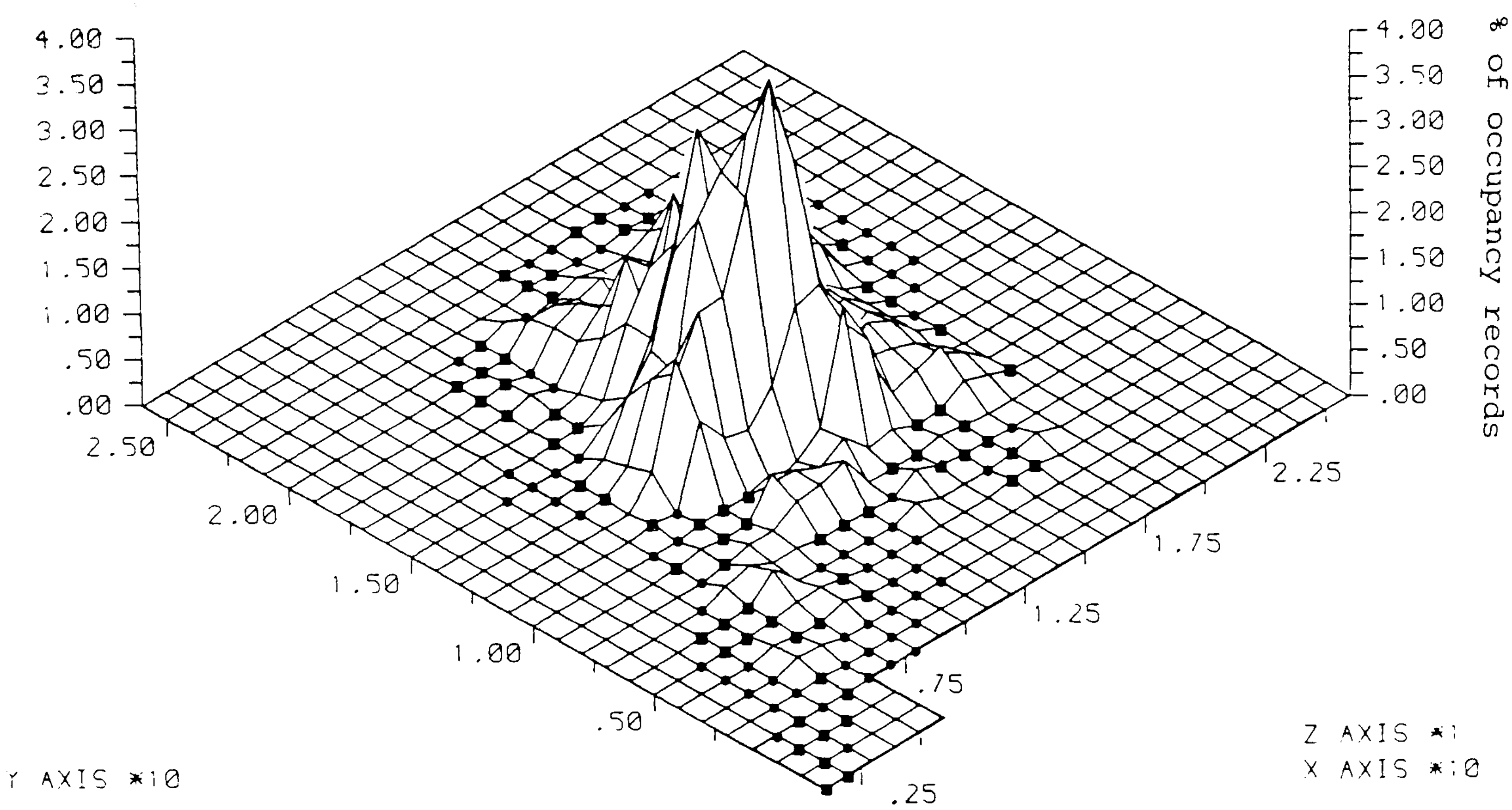


FIG 8.17 FREQUENCY OF OBSERVATION OF NON "C" TROOPS WITHIN "C" ANNUAL RANGE. (see FIG 5.4,MAP 6,7 for base map) GINOSURF PLOT. April 1981-March 1982

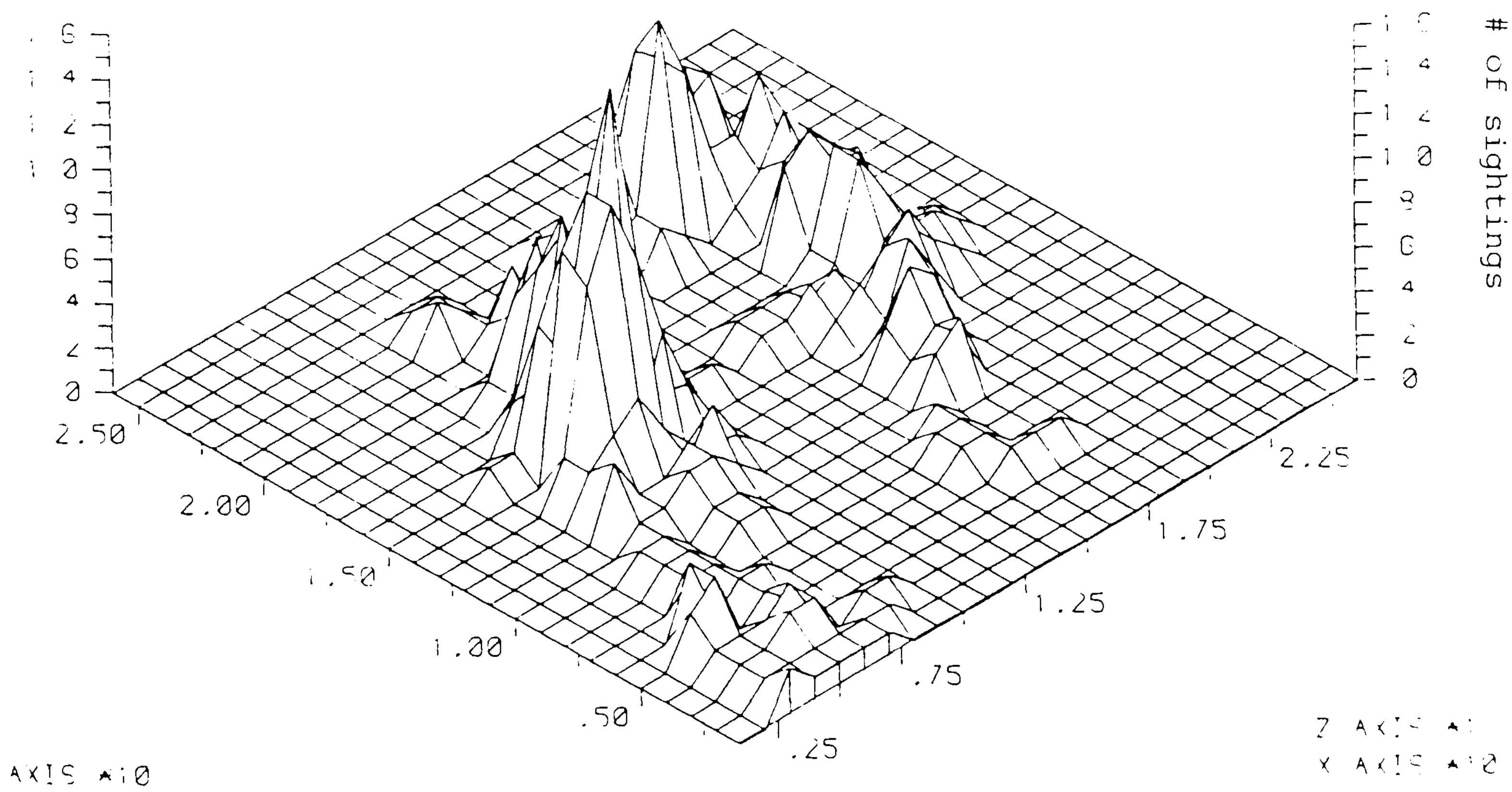
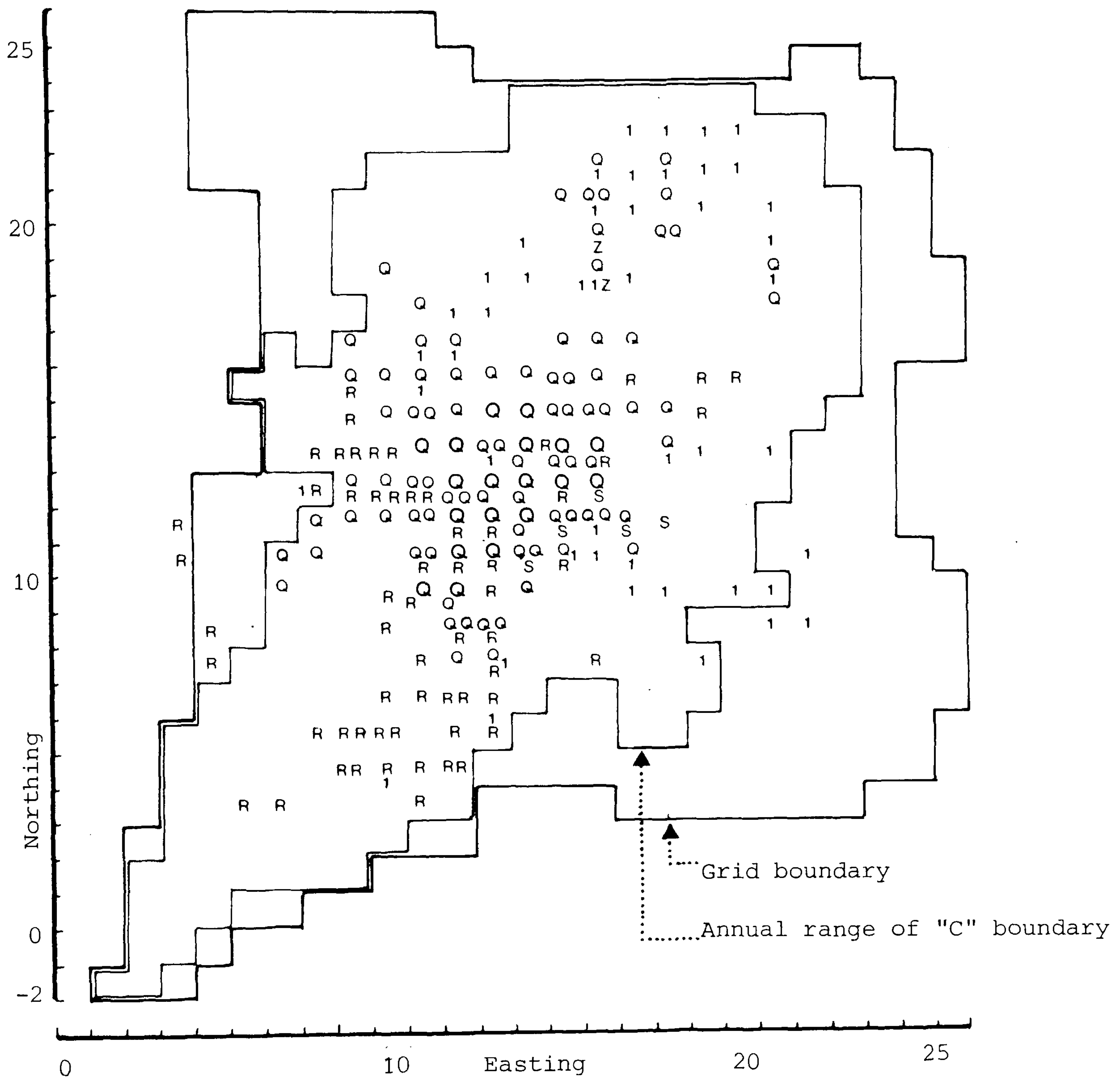


FIG 8.18 FREQUENCY WITH WHICH BANDS OBSERVED IN "C" TROOP STUDY SITE,DURING FOLLOWS: APRIL 1981-MARCH 1982.

(See MAP 6,7 for physical and habitat features)



0 200m Symbol indicates band identity i.e. Q="Q" band. For key of symbol size see FIG 8.15. 1 indicates one observation of an unidentified band.

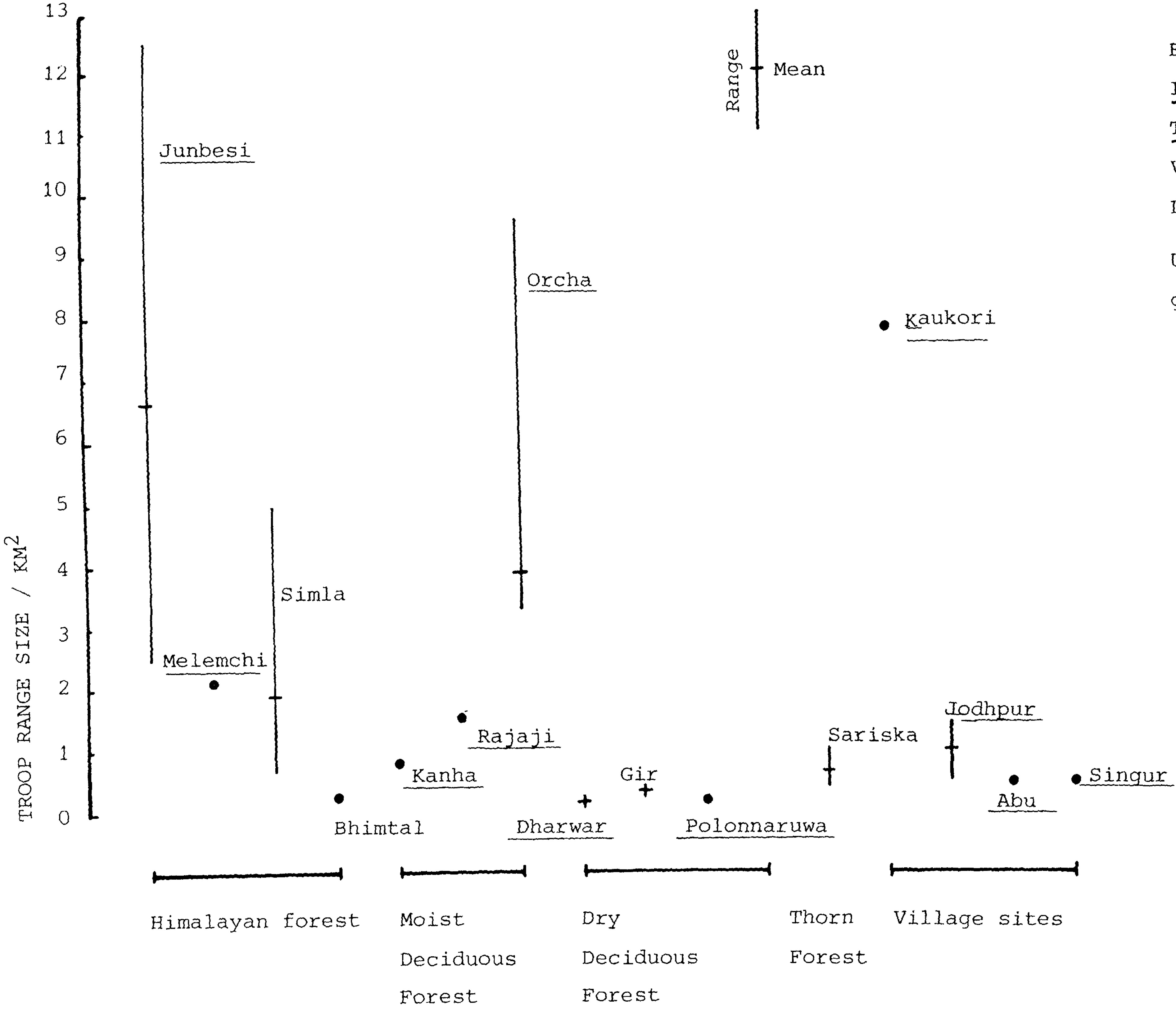


FIG 8.19 INTRA-SPECIFIC VARIATION IN RANGE SIZE OF HANUMAN LANGUR TROOPS. Data from Hrdy (1977b), Vogel (1977), Oppenheimer (1977), Laws & Vonder Haar Laws (1984).

Underlined site=study duration greater than or equal to one year.

FIG 8.20 RELATIONSHIP BETWEEN RANGE SIZE AND DENSITY FOR 15 HANUMAN LANGUR POPULATIONS. (Symbols as in FIG 6.12)

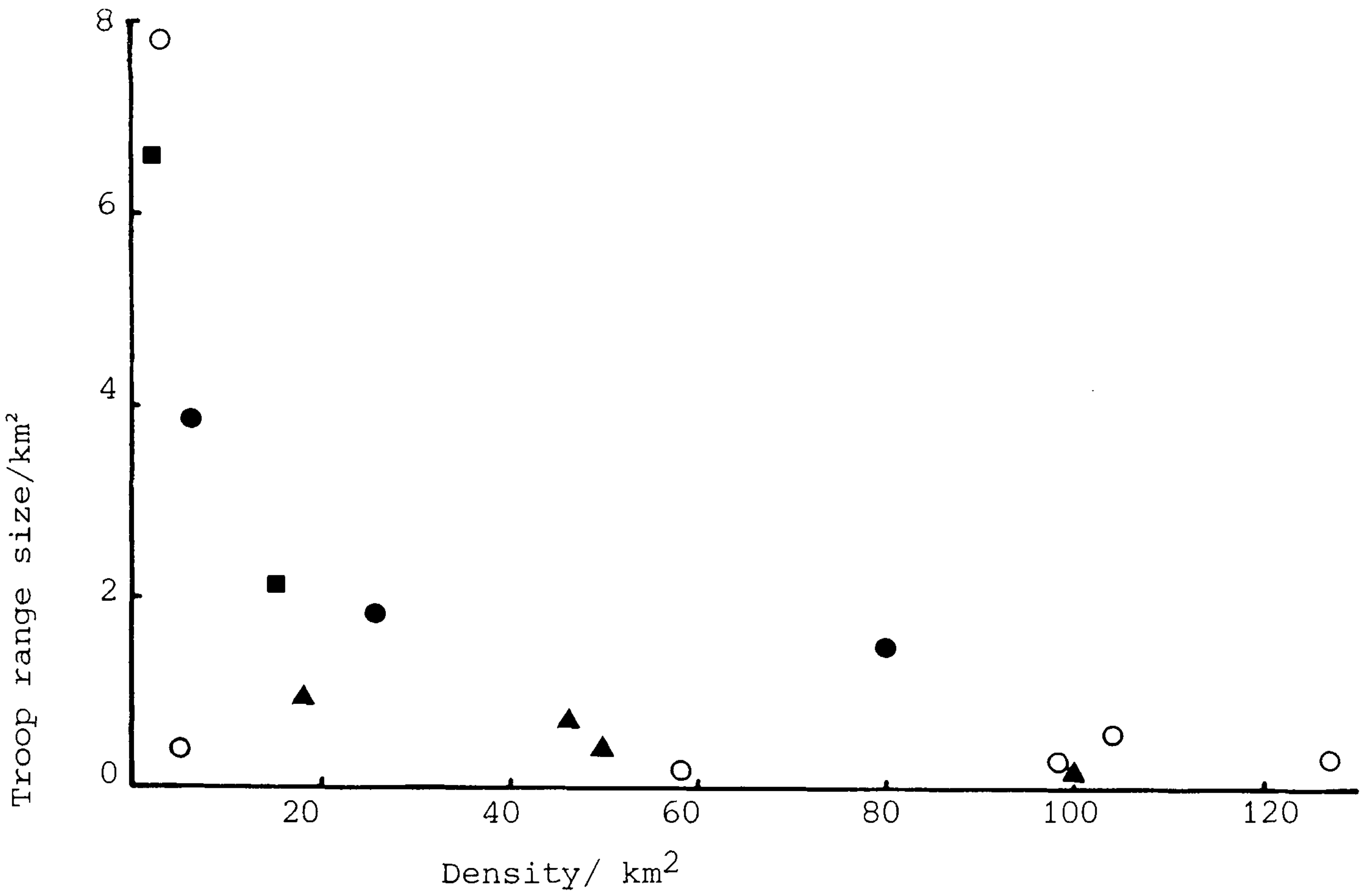


FIG 8.21 RELATIONSHIP BETWEEN MEAN TROOP SIZE AND RANGE SIZE FOR 15 HANUMAN LANGUR POPULATIONS (Symbols as in FIG 6.12).

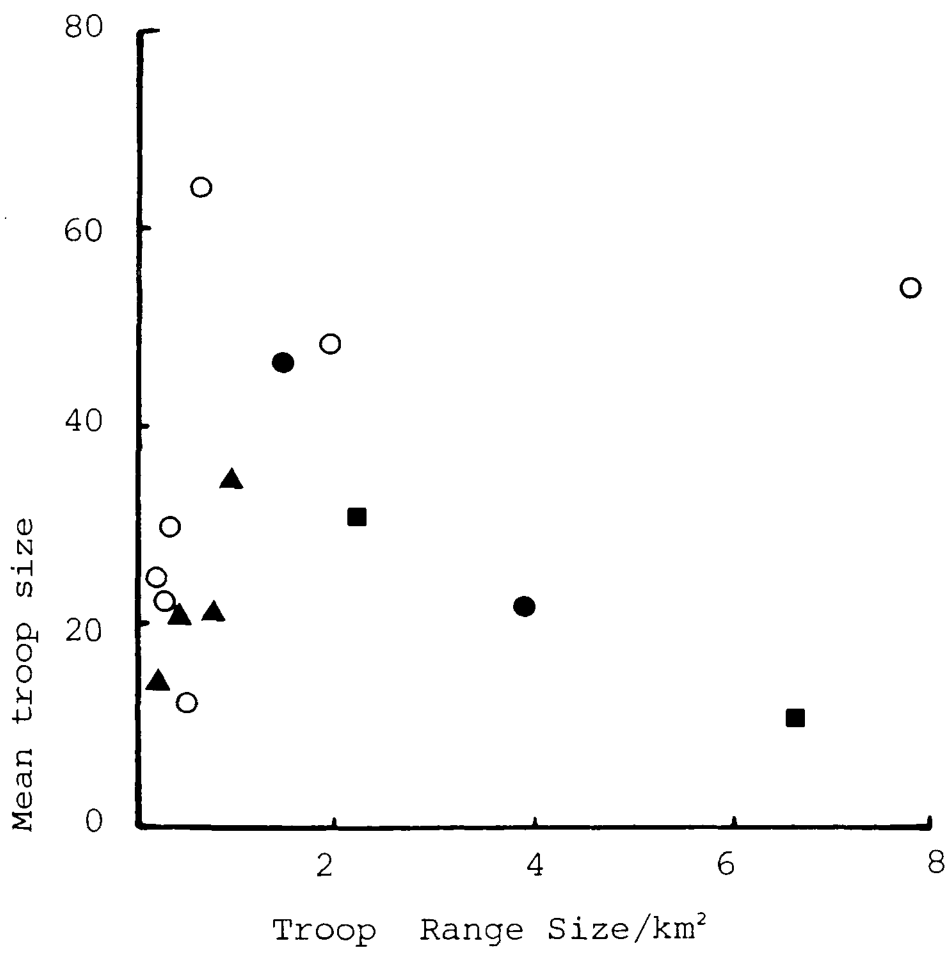


FIG 8.22 MONTHLY VARIATION IN FREQUENCY AND DURATION OF ENCOUNTERS BETWEEN "C" TROOP AND TROOPS AND BANDS.

For encounters with troops and bands and by individual groups.

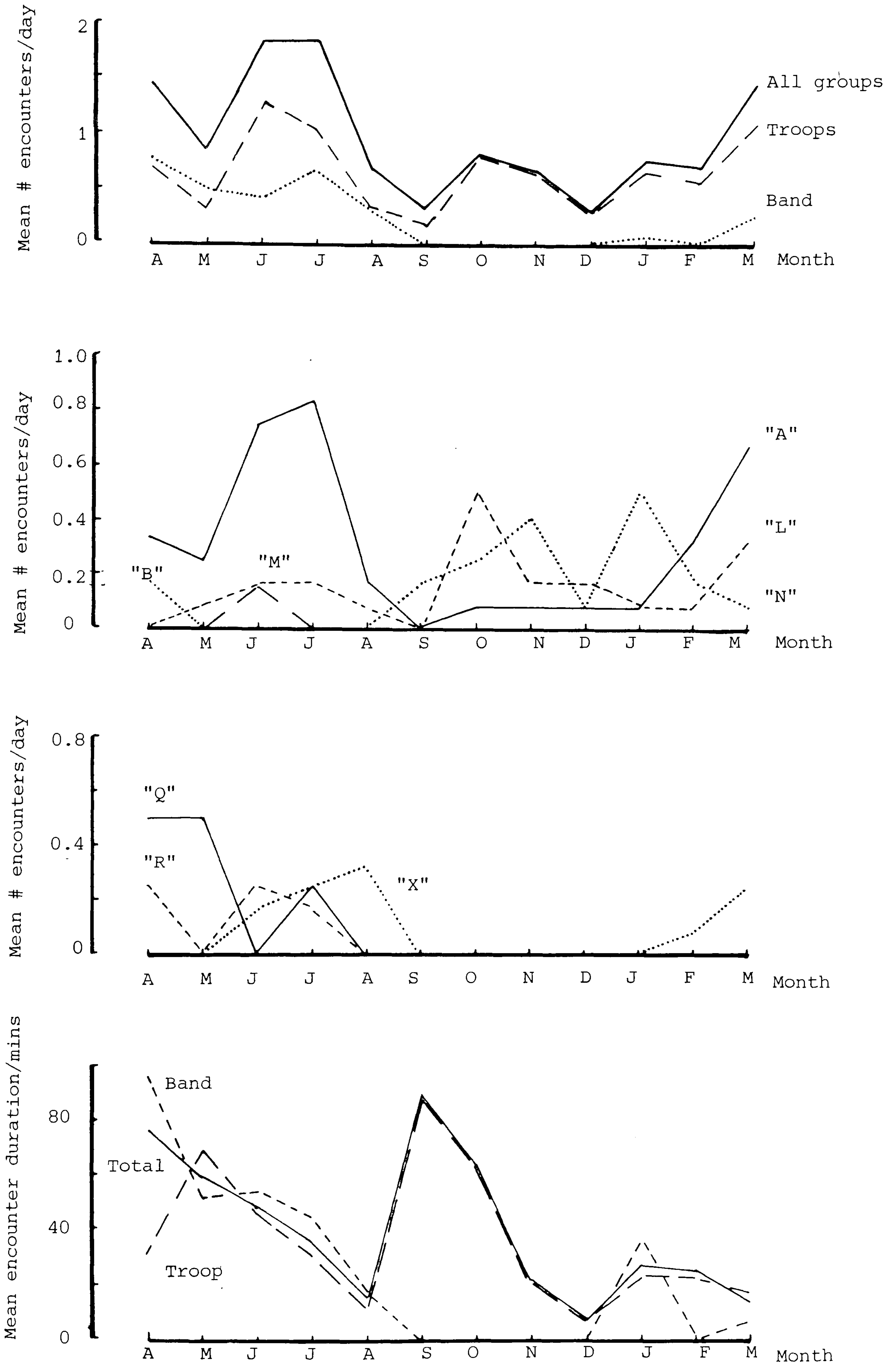
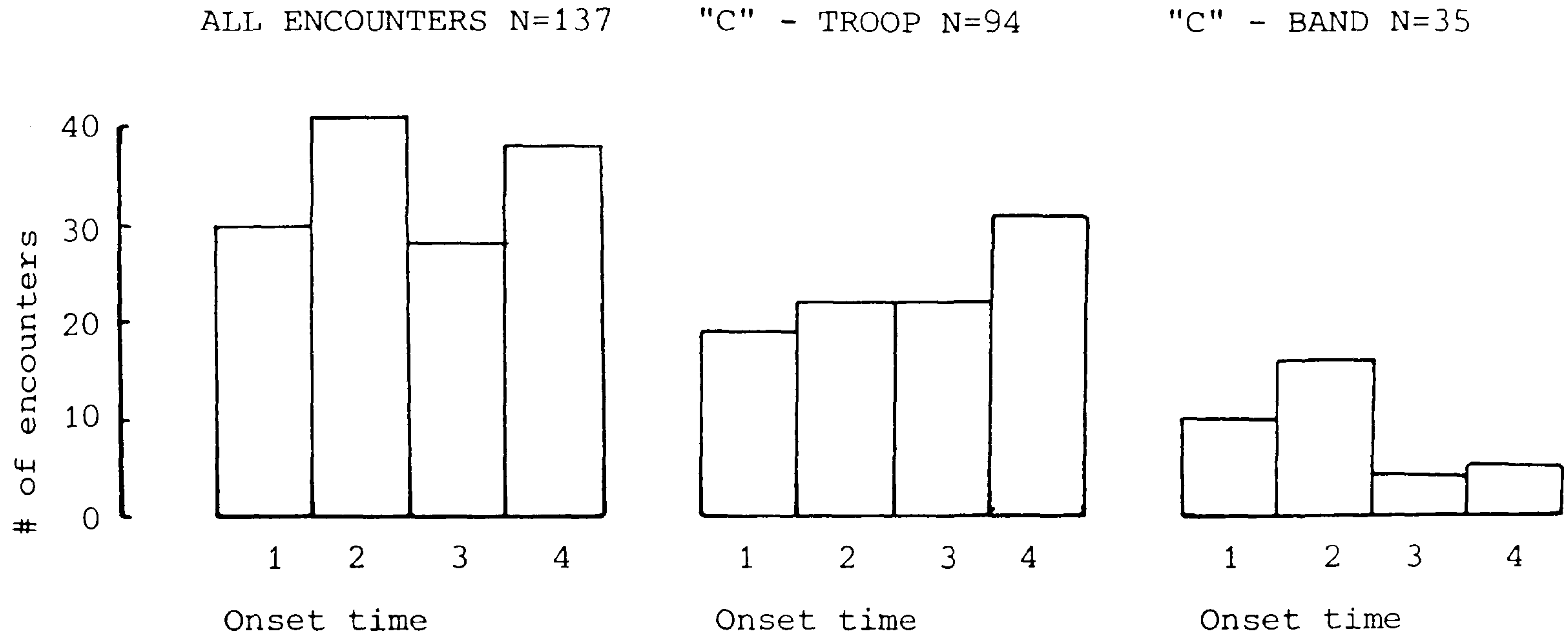


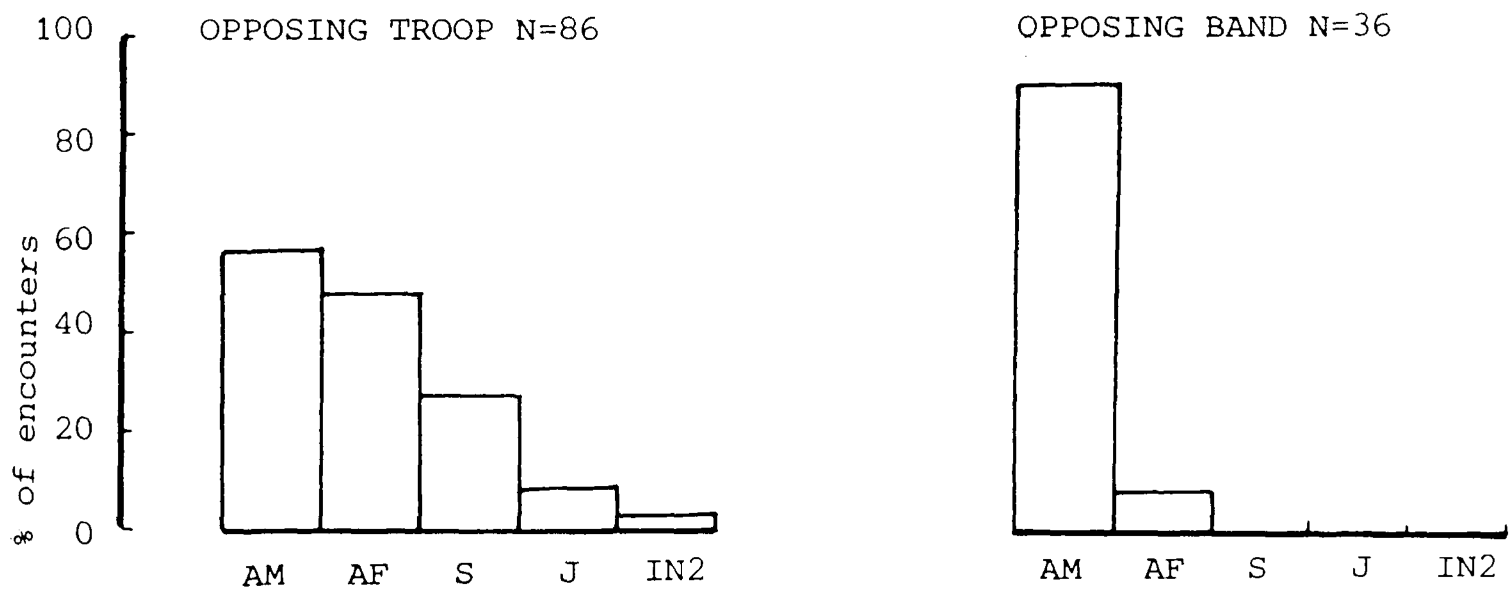
FIG 8.23 DIURNAL VARIATION IN TIMING OF ONSET OF ENCOUNTERS FOR ALL ENCOUNTERS, INTER-TROOP AND TROOP - BAND ENCOUNTERS.



1= first quarter of the day;2= second quarter of the day.
3= third quarter of the day;4= fourth quarter of the day.

FIG 8.24 LANGUR AGE/SEX CLASS PARTICIPATION IN ENCOUNTERS(Age/sex class abbreviations in Table 4.A; "X" = group in encounter with "C")

a) "C" PARTICIPANTS



b) "X" PARTICIPANTS

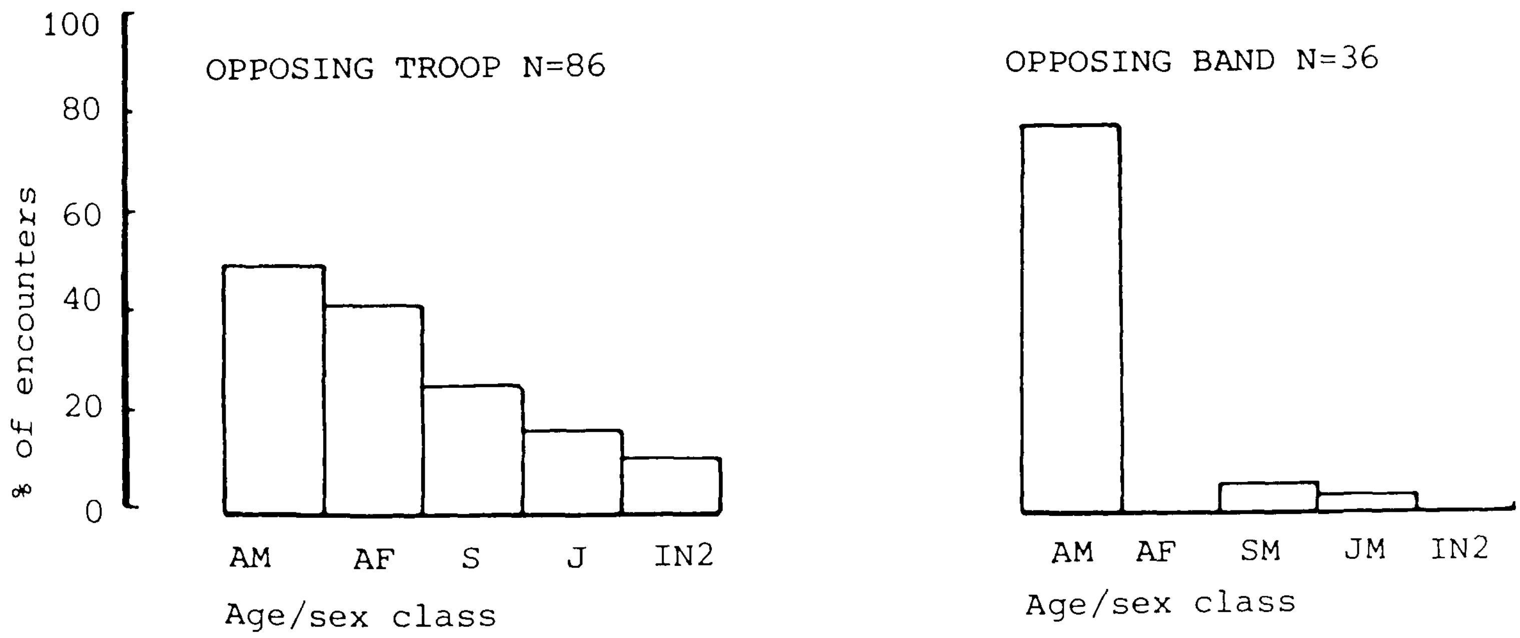


FIG 8.25 FREQUENCY OF BEHAVIOURAL CATEGORIES DURING ENCOUNTERS BETWEEN "C" TROOP AND OTHER TROOPS AND BANDS. Expressed as % of encounters in which behaviour recorded, irrespective of actor.

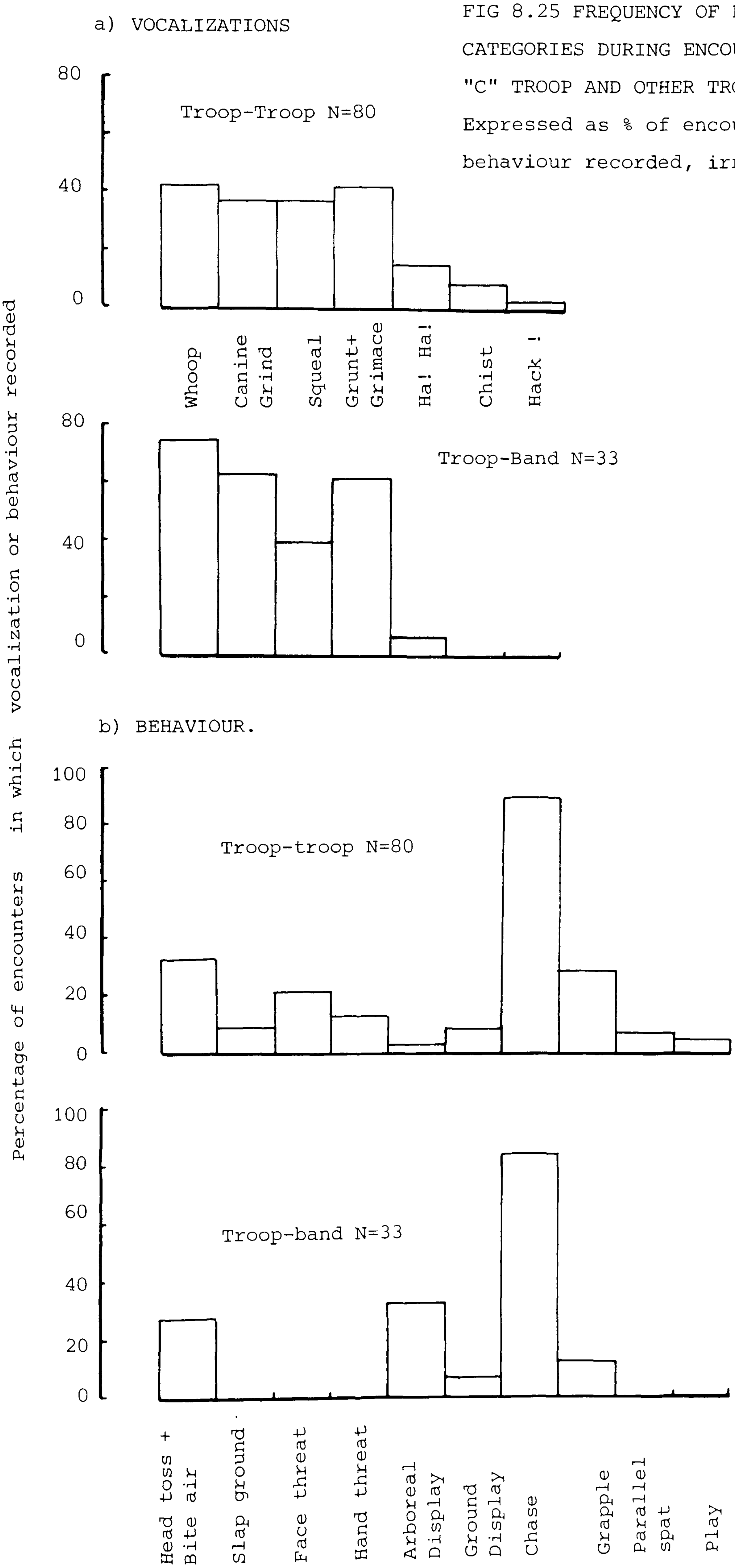


FIG 8.26 SPATIAL DISTRIBUTION OF ENCOUNTERS BETWEEN "C" TROOP AND OTHER TROOPS. 90 encounters shown, recorded on 138 observation days April 1981-March 1982.
# of encounters shown per grid cell, large symbols indicate five encounters. X indicates unidentified troop

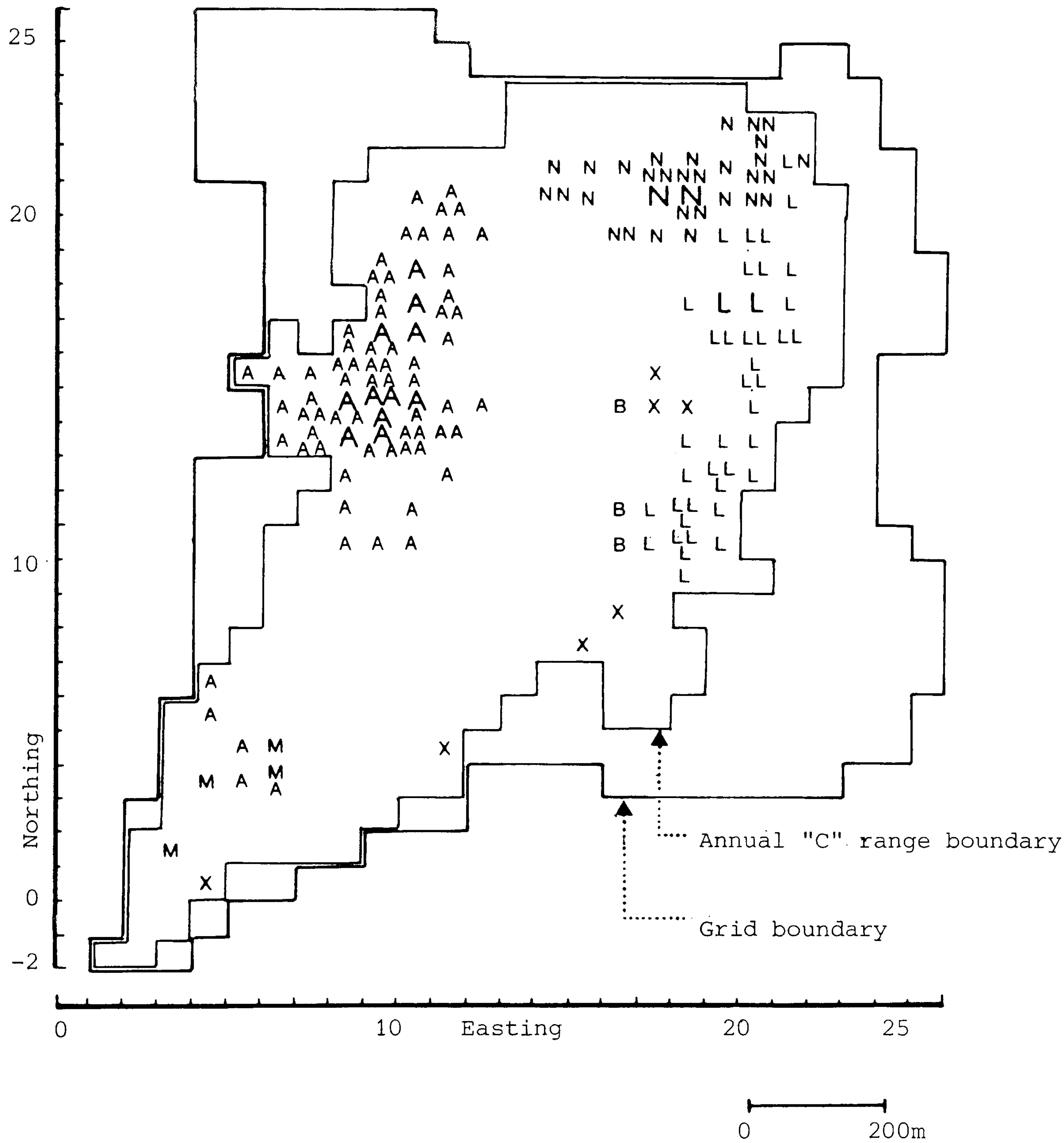


FIG 8.27 SPATIAL DISTRIBUTION OF ENCOUNTERS BETWEEN "C" TROOP AND BANDS. 34 encounters shown, recorded on 138 observation days April 1981-March 1982.
# of encounters shown per grid cell, large symbol indicates five encounters. X indicates unidentified band.

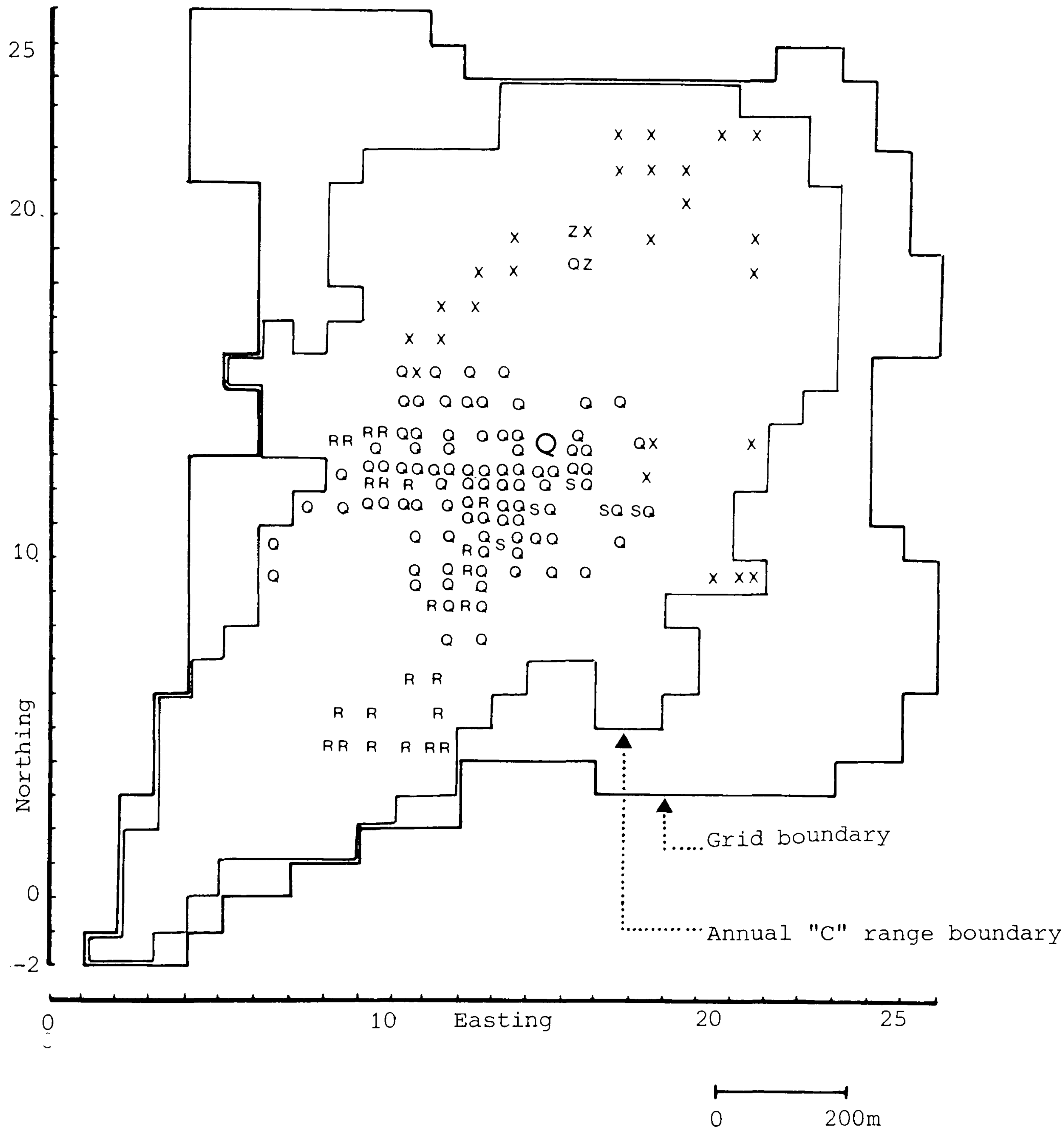
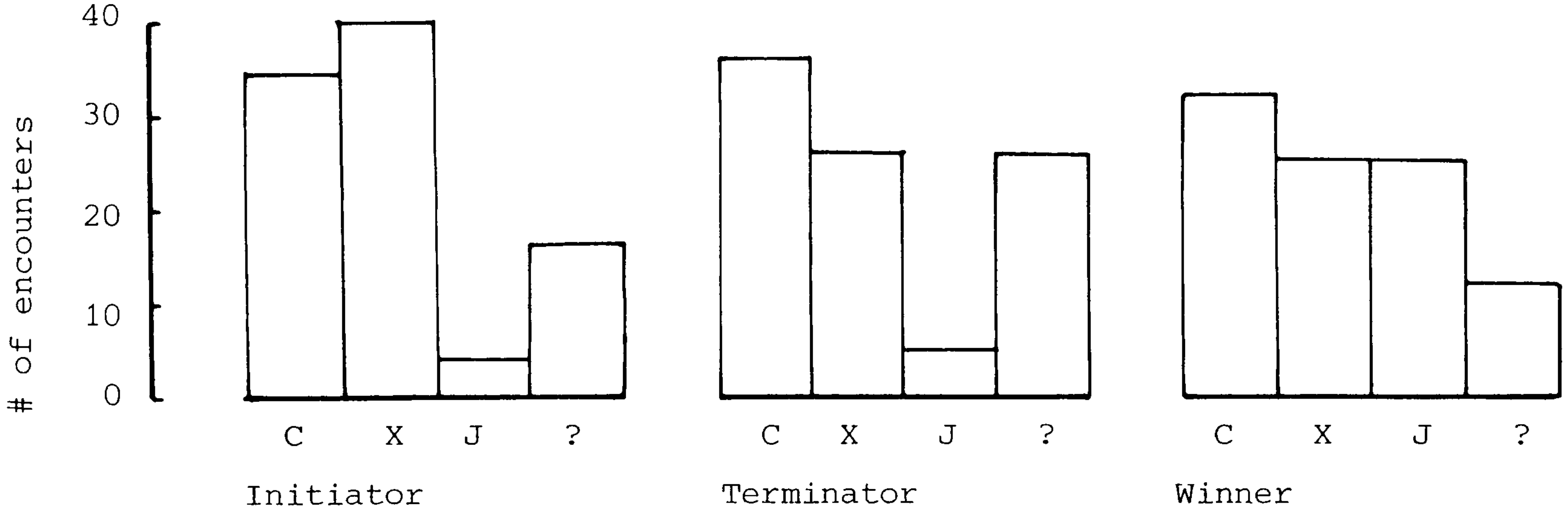
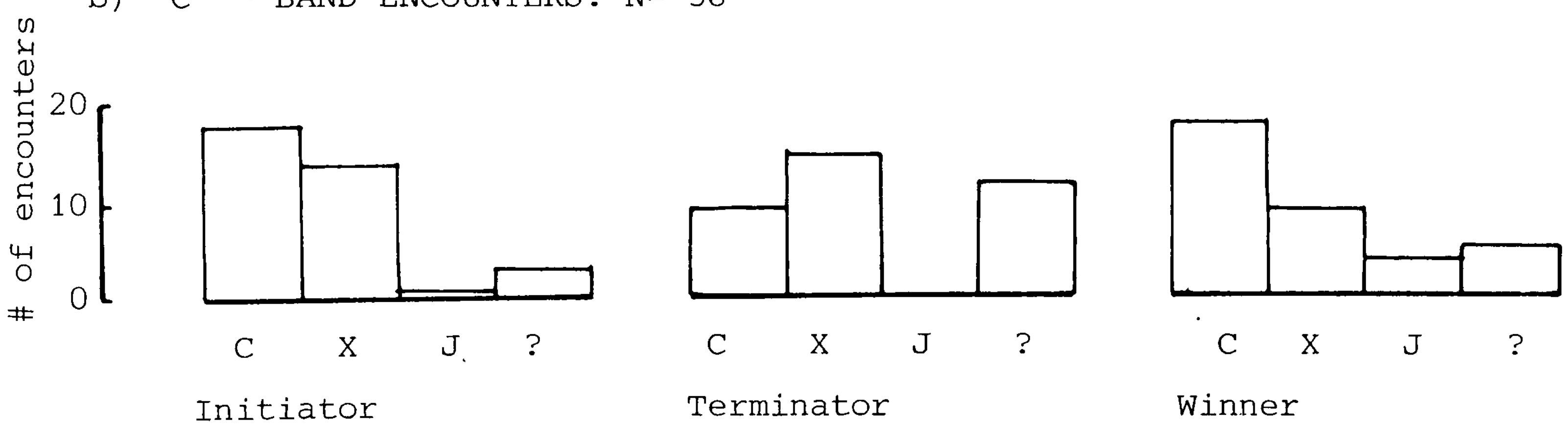


FIG 8.28 FREQUENCY WITH WHICH "C" TROOP AND OPPOSING GROUP INITIATED,TERMINATED AND WON ENCOUNTERS. FOR "C" - TROOP AND "C" - BAND ENCOUNTERS.

a) "C" - TROOP ENCOUNTERS. N= 94



b) "C" - BAND ENCOUNTERS. N= 36



KEY:

C = "C" troop initiated,terminated or won.

X = "X" troop initiated,terminated or won,where "X"=opposition.

J = Joint initiation,termination or or outcome.

? = initiator,terminator or winner not recorded

FIG 8.29/30 VARIATION IN OUTCOME OF INTER-GROUP ENCOUNTERS AS A FUNCTION OF DISTANCE FROM THE CENTRE OF "C" TROOP'S ANNUAL RANGE.

FIG 8.29 "C" - TROOP ENCOUNTERS N= 76.

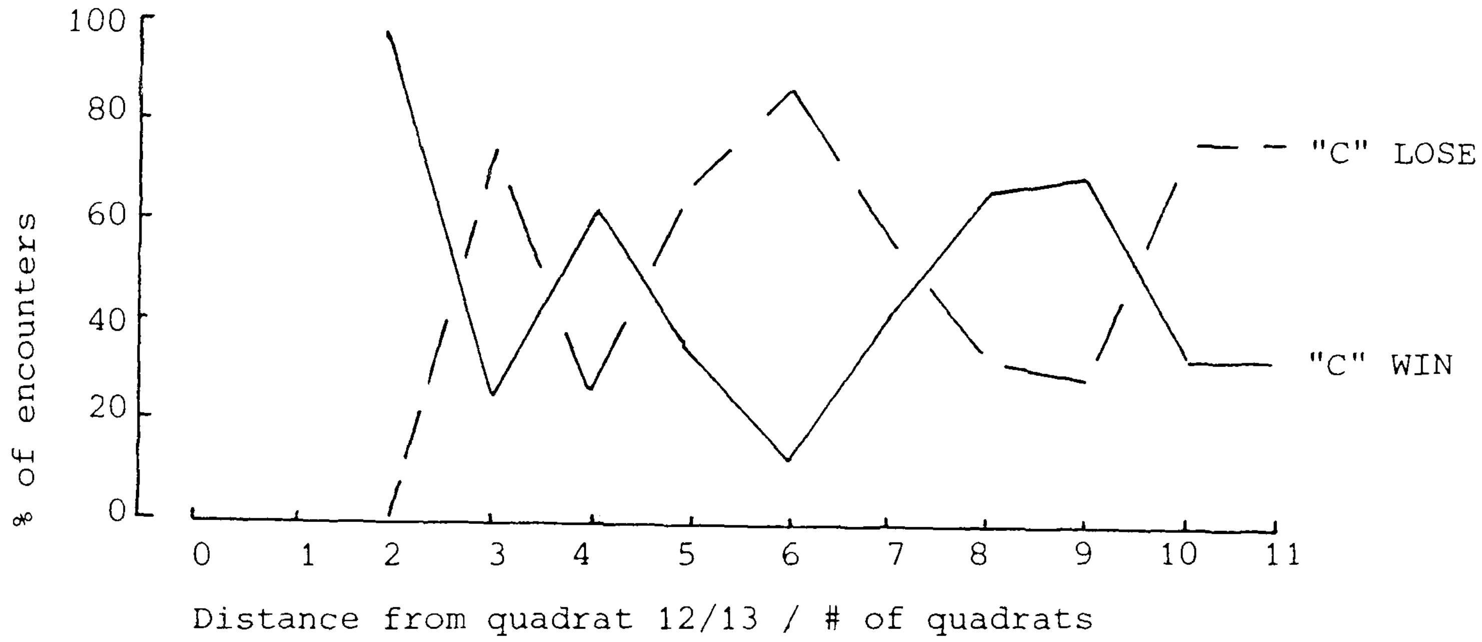


FIG 8.30 "C" - BAND ENCOUNTERS N=25

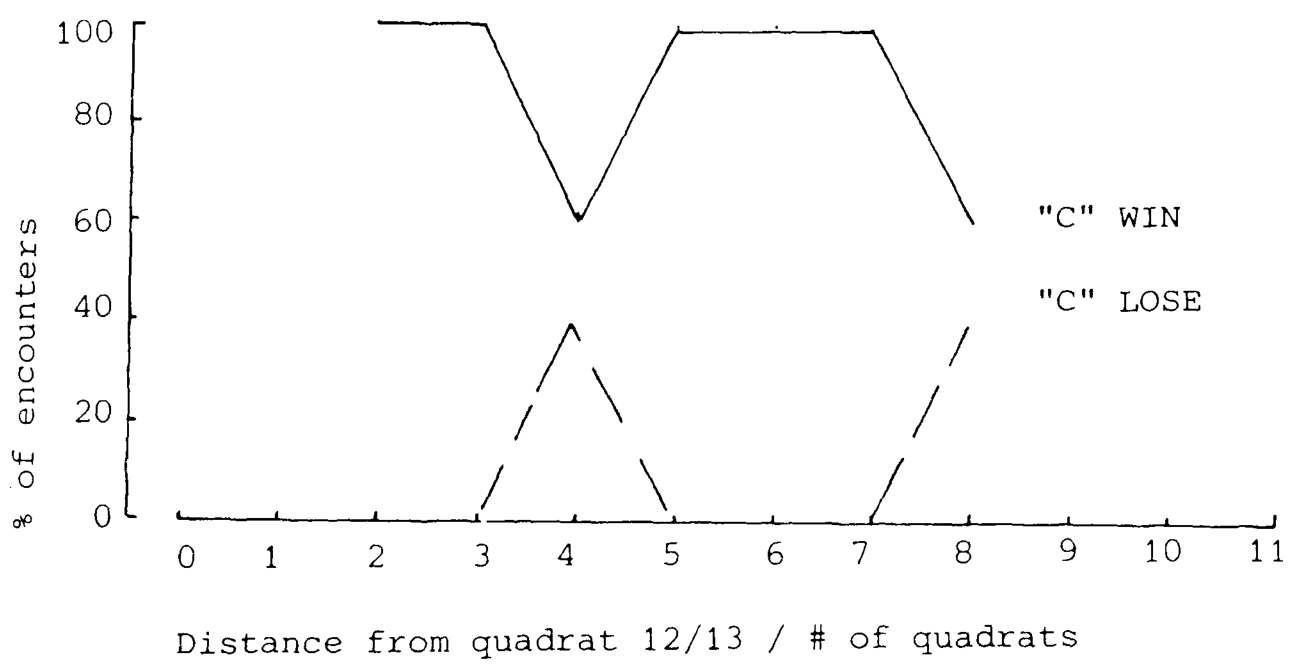
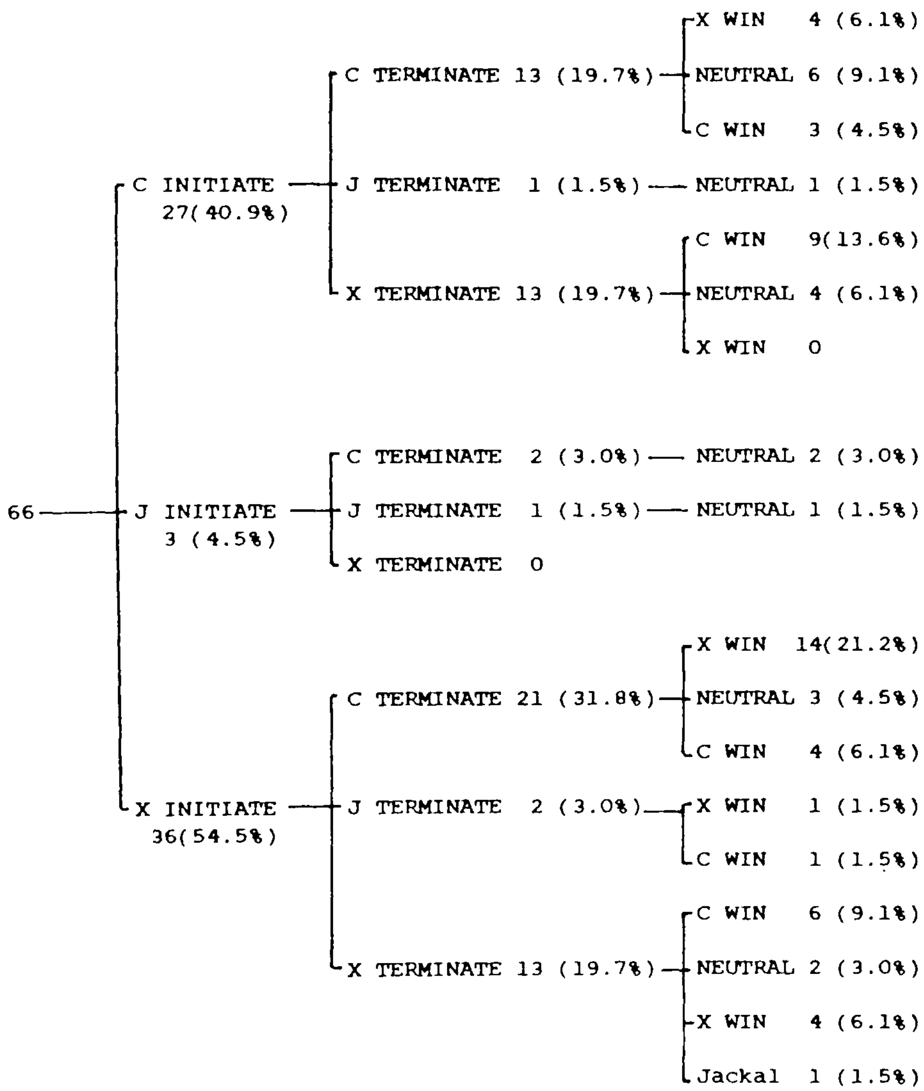


TABLE 8.A SUMMARY OF INTERMONTHLY VARIATION IN INDICES OF RANGING PATTERNS.

Month	#Q/m	H'range	RU	Range overlap	Dispersion	Encounter rate
April	159	4.06	1.594	42.73	3.24	1.42
May	130	3.97	1.409	51.84	2.35	0.83
June	193	4.24	1.208	49.68	2.78	1.83
July	153	4.07	1.576	53.06	3.21	1.83
August	114	3.79	1.447	52.36	3.10	0.67
September	105	3.99	1.565	52.28	2.96	0.33
October	165	4.43	1.183	46.98	2.76	0.83
November	115	3.78	1.436	46.66	2.92	0.67
December	085	3.77	1.235	50.93	2.77	0.33
January	115	4.17	1.091	48.10	2.84	0.75
February	147	4.33	1.347	51.29	2.79	0.67
March	143	4.09	1.198	52.54	2.77	1.42
Mean	135.3	4.06	1.357	49.87	2.87	0.97
± s.d.	30.2	0.21	0.173	3.15	0.24	0.53

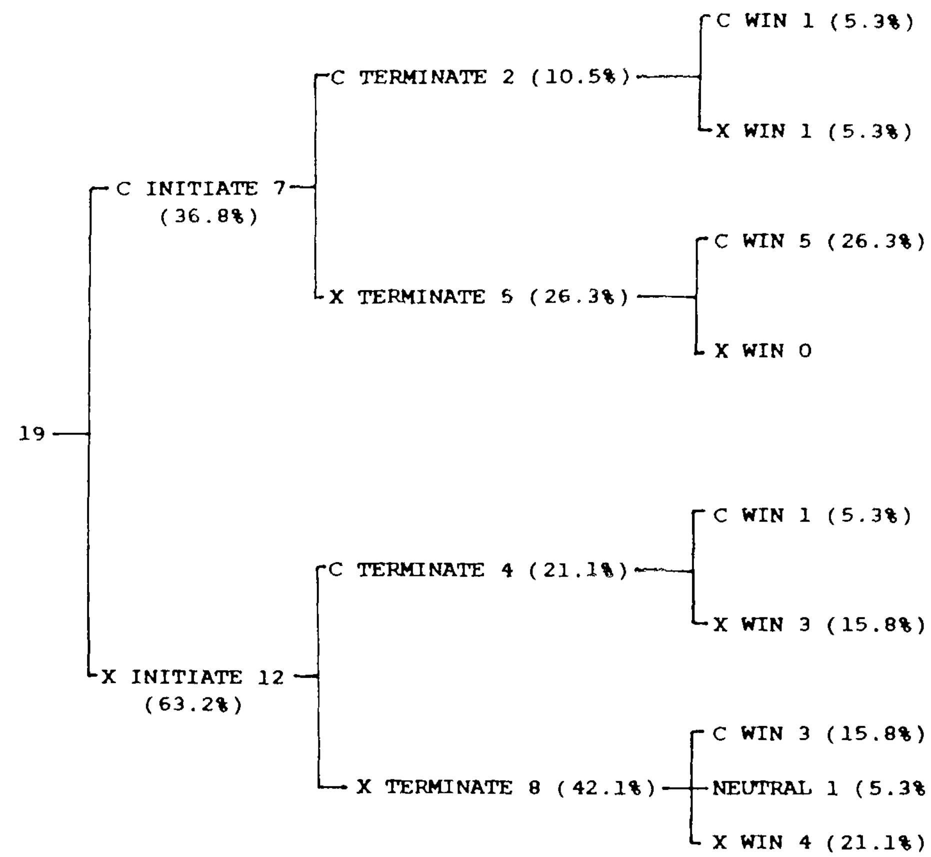
#Q/m =number of different quadrats occupied per month.
H' range =Shannon-Wiener index of diversity for monthly range budgets.
RU =Rasmussens clumping index.
Range overlap =mean % range overlap per month with other 11 months.
Dispersion=mean number of quadrats occupied per scan.
Encounter rate =mean number of encounters between "C" and other groups per day.

TABLE 8.B "C" TROOP–TROOP ENCOUNTER OUTCOME SEQUENCES.
(For 66 encounters)



C initiates	40.9%	C wins	18.1%
		C loses	6.1%
X initiates	54.5%	X wins	28.8%
		X loses	16.7%
C terminates	54.5%	C wins	10.6%
		C loses	27.3%
X terminates	39.4%	X wins	6.1%

TABLE 8.C "C" TROOP–BAND ENCOUNTER OUTCOME SEQUENCES.
(For 19 encounters)



C initiate	36.8%	C win	31.6%
		C loses	5.3%
X initiates	63.2%	X wins	36.9%
		X loses	21.1%
C terminates	31.6%	C win	10.6%
		C loses	21.1%
X terminates	68.4%	X win	21.1%
		X loses	42.1%

PLATE 9

ADULT FEMALE # 39 WITH INFANT #77
MAY 1983, KANHA MAIDAN. AF #45 GROOMS
ANOTHER LANGUR IN THE BACKGROUND

PLATE 10

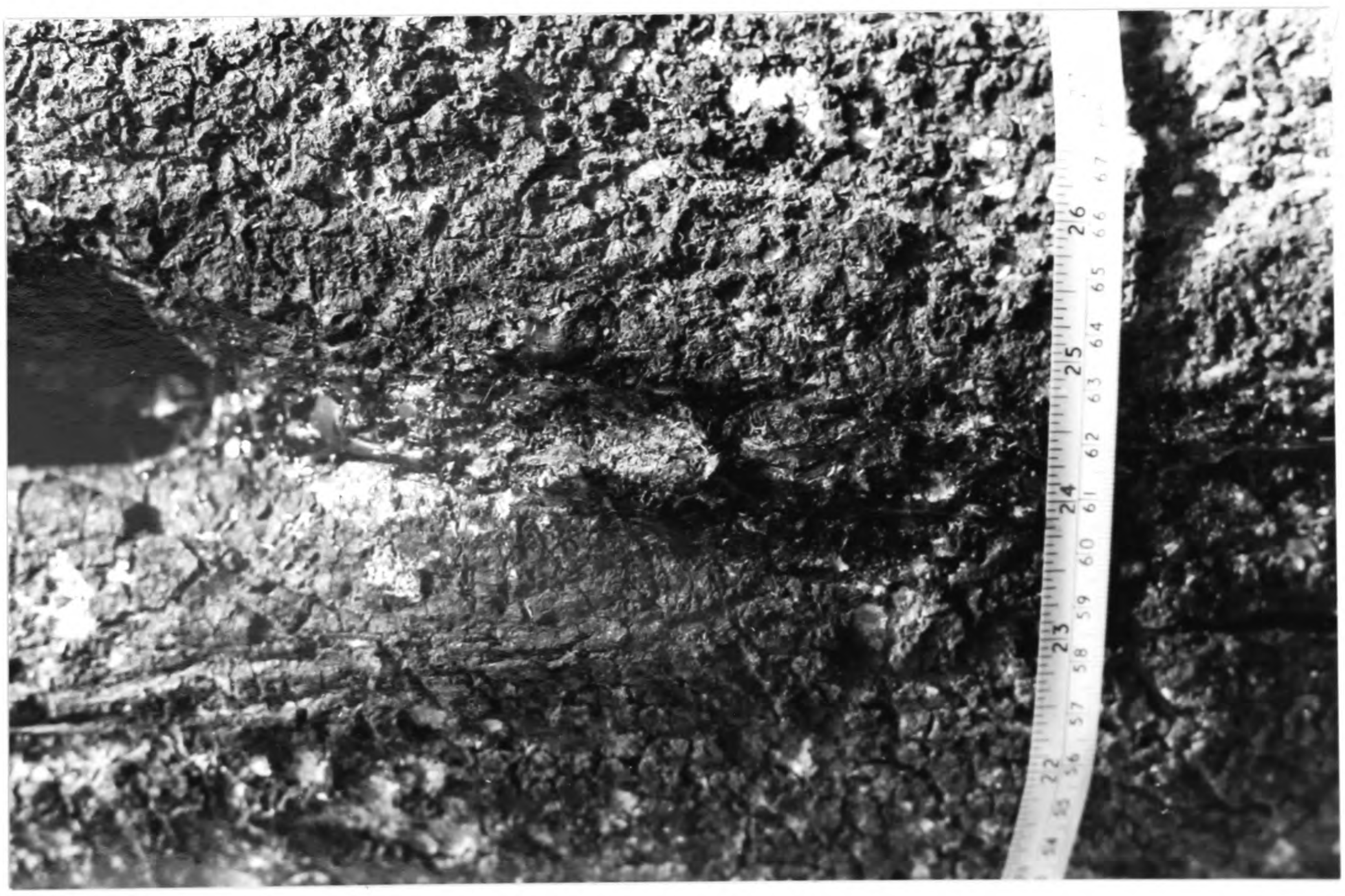
ADULT # 30 FEEDING ON GUM ISSUING FROM
CLEFT IN A Lannea coramandelica BOLE
KULOO CHATTAN.

PLATE 11

A GUM SITE ON A Lannea coramandelica TREE BOLE,SHOWING TOOTH MARKS MADE BY LANGURS (in centre of picture) SCALE IN cm and inches. 17 MARCH 1981.

PLATE 12

SUB-ADULT FEMALE IN "C" TROOP FEEDING ON FRUITS OF Sterculia urens. KULOO CHATTAN. 5 MAY 1981



CHAPTER 9

FEEDING ECOLOGY

CHAPTER 9 FEEDING ECOLOGY

9.1 INTRODUCTION.

Feeding ecology is the fifth aspect of langur biology considered in this thesis which with activity, ranging, social organisation and vegetation forms an integrated study of potentially inter-related factors. In this chapter feeding budgets by species and by items will be presented and the particular cases of gummivory and insectivory and drinking considered. Feeding is discussed here in isolation; it will be integrated with other aspects of langur biology in Chapter 10.

The feeding ecology of langurs has been investigated in detail at only a few of the many sites at which entellus has been studied; research effort has concentrated on social organisation and social change. Yoshiba (1967) studied the diet of langurs inhabiting dry deciduous forest at Dharwar. Oppenheimer (1978) and Makwana (1977) published short accounts on the diet of langurs at Singur and Jodhpur respectively. Ripley (1970) considered the sociology of foraging and provided a diet list for Polonnaruwa. The most detailed study published is that of Hladik (1977), also for Polonnaruwa, which provides detailed information on annual and monthly feeding budgets in terms of quantity of food ingested. Hladik also investigated the nutritional value of items and the quantity of food resources available in the troops range. However, in no langur study has activity, ranging, feeding, vegetation structure and phenology been investigated concurrently in the way exemplified by numerous African primate studies (e.g. Clutton-Brock 1972, Marsh 1978, Oates 1974, Waser 1977a, Rudran 1978, Struhsaker 1975).

9.2 METHODS.

Clutton-Brock (1977b) summarized the methods that can be used to quantify diet compostion in primates:

a/analysis of stomach contents.

b/analysis of dung samples.

c/visual measurement of amounts of different foods eaten.

d/measurement of frequency with which different foods are chosen.

e/measurement of proportion of feeding time spent on different foods.

The first two methods were impractical in this study, the former because it was inconsistent with a long term study and the latter because of difficulties in analysis and in correlating its quantitative relation to diet. The visual measurement of ingestion as used by Hladik (1977), although probably providing the most pertinent and reliable information, is overwhelmingly difficult to record in conditions of poor visibility. The frequency method as used by Struhsaker (1975) requires constant awareness of the identity of individual monkeys and is perhaps bedevilled by more potential bias than the measurement of feeding time. Here the measurement of proportion of feeding time spent on different species and different items was used, recorded during scans. This method has the advantages of relative simplicity, robustness to variation in methodology and the availability of tests for bias (Clutton-Brock 1972). It has been one of the commonest methods used in primate field studies, thereby facilitating comparison between langurs and the cercopithecids of East Africa. It potentially suffers however from visibility bias and feeding time bears an unknown relationship to the actual quantity of food ingested because of variation between categories of food in feeding rate and item size. For example, for equivalent amounts of time spent feeding on mature leaves and leaf buds we would expect a considerably larger mass of mature leaf to be ingested than of buds. Hladik (1977) showed that the results produced by the two methods were not well correlated for Singalese Hanuman langurs. However, with langurs feeding 30m up trees it was obviously impractical to measure mass ingested. Studies in which feeding time and frequency have been recorded concurrently have shown that they produce rather similar results (Marsh 1981c, Oates 1977a).

The feeding data were collected during scans, as described in 7.2, at half hour intervals from dawn to dusk for seven days a month (SCAN and DROP follows combined; see Chapter 3). For each animal recorded as feeding during each scan the food item and food species were noted. The tree species present in the study area and their abundance, i.e. the resources available, are described in Chapter 5. The major categories of food item recognised followed the same typology as used in phenology recording (see 5.2). In addition, the following categories were recognised :

Stem	
Petiole of mature leaf	Herb seed
– – young leaf	Grass seed
– – unknown age	Earth
Leaf of unknown age	Invertebrate
Bark	Gum (plant exudate soluble in water)
Herb	Resin (plant exudate insoluble in water)

All tree species, from which langurs utilized exudate, produced either resin or gum. Therefore, such feeding from a gum producer was classed as gummivory and from a resin producer as resin consumption. The scan data were used to calculate feeding budgets for each month and for the twelve month cycle in terms of time invested in feeding on items and species. As these budgets are generated from scan data the discussion of bias and methodology, in Chapter 7, applies.

9.3 FEEDING BUDGETS : RESULTS.

9.3.1 ANNUAL BUDGET AND BIAS.

The annual budget (from April 1981-March 1982) was expressed, in the manner of Waser (1977a) and Oates (1977a), as the number of feeding records per species or item as a percentage of the total number of feeding records (N=6787). Because of the smaller sample size in September (see 3.2.1) the budget for that month was weighted by 7/6 in compensation. The budgets by items and by species and items are tabulated in Tables 9.A,9.B and depicted Fig 9.1 & 9.2. The species of herb and grass consumed are tabulated in Appendix V.E.

The Hanuman langur is usually referred to as a folivore or leaf monkey. Indeed leaf, especially mature leaf, was the predominant item in terms of feeding time. Leaves, buds, stems and petioles combined contributed over half the diet. However, fruits at 24.5 % made up a significant portion of the feeding budget. Flowers and flowerbuds contributed 6.6 % and 2.9 % respectively. The food item was unidentified in 6.8 % of the records. Of 68 species of tree and woody climber in "C" troops range the langurs were observed to feed on 53 species during scans and 60 during follows. The species from which no items were consumed were *Adina*, *Casearia tomentosa*, *Cordia macleodii*, *Garuga*, *Kydia*, *Randia*, *Butea superba* and an unidentified bush in Q 16/05. Only invertebrates were taken from *Lagerstroemia*, *Tectona*, *Cassia*, *Grewia* and *Glochidion*. Of the seven major phytophases (those listed in 5.2) langurs only used all from one species, *Mallotus*. Most commonly langurs utilized four items (13 species) or only one (9 species). Mature leaf was taken from 26 species of tree and climber and fruit from 34. In April 1981 troop langurs were seen to scoop up and eat filamentous algae from the Deotalao lake (see 3.1.2).

The two top ranking species in the annual diet were Pterocarpus and Shorea, which combined contributed 24.3 % of feeding time. Although the diet was diverse in terms of the total number of species utilized, feeding was concentrated on relatively few. Only the top 22 species ranks contributed more than 1 %. The top 12 species contributed 70 % of the diet. The Shannon-Wiener diversity index,H', for the annual budget (Table 9.B) was 3.157. This index reflects both the number of dietary items and species and the evenness of their use (Harvey 1977). Terrestrial feeding represented 13.2 % of the annual diet.

However, as was the case for activity data (see 7.3.1) the budget could have been biased by association between the food items consumed and the number of feeding langurs recorded per scan. By analogy with Clutton-Brock (1974b), I gained the impression that, for example, I scored more animals feeding on Sterculia fruits than Shorea fruits in proportion to the actual number of animals feeding. This was a consequence of gross differences in leaf density and hence visibility between the two species. The potential bias was tested using the same technique as used in 7.3.1, derived from Clutton-Brock (1974b), in which the data collected in each scan are treated equally. This equalisation was carried out for May, August and December (i.e. one month per season). For each month and for the ten species on which "C" troop fed the most, the number of feeding records per species were expressed as a percentage of the total number of records of langurs seen feeding in the scan. The mean of these percentages was taken for each follow and the median of these means calculated for each month. This yielded a measure (Method B) of the percentage utilization of ten species for each month in which each scan has equal weight. These budgets were compared with the relevant monthly budgets as calculated in 9.3.2 (Method A). As is shown in Fig 9.3. the two estimates are highly correlated (May: r_s=0.950, n=12, p<0.001, August: r_s=0.908, n=12, p<0.001, December: r_s=0.976, n=12, p<0.001). This result, though it does not show that such bias does not occur, does indicate that there was no strong determining association between the number of animals seen in scans and the structure of the tree being fed in.

The annual budget was calculated irrespective of variation in the monthly sample sizes. However, as shown in Table 9.A. there was inter-monthly variation in the number of feeding records and consequently some months will tend to be over-represented in the annual budget. Therefore, the alternative calculation, the mean of monthly percentage budgets, as used by Marsh (1981c), might be more appropriate. The decision can be resolved by considering the sources of variability in sample size, which are potentially:

a/variation in observer effort.

b/seasonal variation in duration of dawn-dusk follows.

c/feeding langurs more visible in certain months.

d/differences in proportion of time spent feeding.

With a corrected September budget a/ is not applicable and sample size variation is the inverse of what would be expected if b/ was a determining factor. The test for bias given above suggests that c/ is unlikely to be important. However, as described in 7.3.2 there is pronounced inter-monthly variation in the proportion of time spent feeding. Consequently, to equalize months would under-estimate the contribution the prolific feeding months make to the annual budget. In terms of species composition, the annual budget would appear to be representative of langur diet as a curve of cumulative number of species consumed with accumulated observation time (Fig 9.4) levels off towards an asymptote after some six months.

9.3.2 MONTHLY VARIATION.

Langurs of "C" troop showed considerable inter-monthly variation in feeding budgets in terms of both items and species (Table 9.A,9.C). Monthly variation in proportion of time spent feeding on the various items is shown in Fig 9.1. A number of monthly indices of feeding behaviour are given in Table 9.D. In the cold weather months of November to February mature leaves were consumed prolifically whilst open and closed leaf buds became important towards the end of the season. In the hot weather, from March to May, flowers and flower buds were important in the early months and fruits in the later months; leafbuds and young leaves contributed small quantities. Mature leaves were noticeably absent from the diet. With the onset of the monsoon in June the diet differed little from that of the hot May but in July the feeding changed markedly with mature leaves and their petioles becoming important. Considerable quantities of invertebrates were consumed in the early monsoon months and a moderate amount of fruit. The proportion of mature leaves steadily increased until October when fruit consumption, from shrubs (Flamengia) and not trees, again became predominant.

The monthly budgets also showed considerable variation in the species composition of the diet. Monthly variation in percentage of time spent feeding on some important food species are shown in Fig 9.5 & 9.19,19. The most consistently utilized species was Shorea, which was annual rank 2 and consumed in all months (Fig 9.5). The lowest rank it reached was 14 and it showed three top ranks and two second ranks. In contrast, the annual top rank Pterocarpus was fed upon for a much more restricted part of the year,the cold weather, when it was in full mature leaf. In utilizing Shorea langurs fed on a wide variety of items, eating different categories in different seasons. In a few species, such as Mallotus, the same item (open leaf bud) was consumed throughout the year.

However, most species were fed upon for only a restricted period with only one major item consumed. This pattern was most extreme for the shrub Flamengia semilata which was rarely utilized outside October when feeding on its fruits contributed 61.9 % of the diet and was related to a peak in terrestrial feeding.

As noted in 9.3.1. a few species were used extensively whilst most were used very little. The distribution of percentage feeding time per species in descending rank order for the top 10 ranks is shown in Fig 9.6 for each month. There is a dramatic contrast between October with its preponderance of Flamengia feeding and July with a considerably more even distribution. The Shannon-Wiener diversity index, H' was calculated for the monthly budgets. For both items and species-specific items monthly variation in H' (Fig 9.7) suggests that the diet was more diverse in the early monsoon than in the late monsoon and cold weather. The hot weather was intermediate. High diversity was associated with periods when the diet was not dominated by mature leaves, flowers or fruits.

The percentage overlap between the diets was calculated, in terms of items and species-specific items, in the manner of Holmes & Pitelka (1968) as used in 8.3.2 and portrayed in single-linkage dendrograms produced by CLUSTAN (Wishart 1982,see Fig 9.8,Appendix V.G). Both plots suggest that March, April and July were the most dissimilar months. The rest of the year tended to cluster into contiguous months with December and November, June and July being particularly similar pairs. The months from August to February tend to form one large cluster in both items and specific items. Therefore, there is a tendency for adjacent months to be similar to each other and for the late monsoon and winter diets to show extensive overlap between months.

Inter-monthly variation in the use of minor dietary components is shown in Fig 9.9 & 10. Invertebrates were observed to be consumed during the monsoon and winter months, with a peak in the early monsoon, when they constituted 24.9 % of the diet. Invertebrate foraging is considered in more detail in 9.6. Petioles were mostly taken from mature leaves, resulting in a considerable drop of lamina to the forest floor. The seasonal pattern of petiole consumption was similar to variation in mature leaf feeding which, apart from a fall in October, was most frequent in the monsoon and winter. Stem feeding occurred in all seasons but again was most frequent in the winter and monsoon. If the consumption of gum is measured as the percentage of feeding time and also as the frequency of opportunistic observations of langurs feeding very similar patterns result (see Fig 9.10). The pattern is bimodal, peaking in the hot weather and monsoon with little feeding at the outbreak of the rains or in the winter. Gum consumption is considered in more detail in 9.5. Feeding on earth, mostly from termitaria or termite re-worked soil on logs, occurred in most months but was especially frequent in August. On three occasions in August and October "C" fed at stream bank saltlick at Q 20/20 (see Map 7) and fed extensively on the clayey soil, un-reworked by termites. This saltlick, also used by ungulates, is probably of natural origin but has been supplemented by the provision of saltlick blocks by the Forest Department. In May a langur partially consumed a mud ball built by a hymenopteran (Delta sp.,Eumonidae) on a C.myxa twig.

Feeding on tree bark was most prevalent in the monsoon and late winter with none being observed in the hot weather. Herbs, from both the forest floor and meadow, were fed upon from September to February, probably reflecting the annual phenology pattern. Herbs and grass seeds were consumed in the late monsoon, the season of reproduction in low stature plants. The seeds of the herb Plectrocanthus icanus, which form dense beds beneath trees, were the most commonly utilized.

9.3.3 SPECIES SELECTION RATIOS.

As shown in Chapter 5 there was wide variation in the abundance of tree species within "C"'s range, with a few species very common but most rare. Similarly, as shown here, there was wide variation in the feeding time per species with a few consumed prolifically but most rarely utilized. The extent to which these are related, i.e. whether tree utilization is a reflection of their abundance, can be estimated by calculating a selection ratio (Clutton-Brock 1977c). A selection ratio is the ratio of % feeding time per species to a measure of the species abundance. Here tree relative dominance, % ABH, (see Chapter 5) is used :

$$\text{Selection ratio species}_i = \frac{\text{\% of feeding records in annual budget for species}_i}{\text{relative dominance of species}_i}$$

This ratio suffers from the following potential disadvantages:

a/relative dominance is unlikely to be linearly related to canopy size across species.

b/relative dominance is a poor estimate of food availability.

c/the ratio does not take into account variation in phenology and biomass between different items.

d/feeding time is probably poorly related to the quantity of food ingested.

Although crude, the ratio provides a means of gauging gross differences in selection and is particulary useful in identifying cases were animals show strong selection for rare tree species (Clutton-Brock 1977c). The ratios for the top 30 ranks in the annual diet are shown in Fig 9.11. The distribution shows a tendency to be skewed to the left, peaking at rank 4 with a minimum at rank 2, the omnipresent Shorea. The most strongly selected species, in descending rank order of the ratio, were Anogeissus, Bauhinia retusa, Ehretia, Ficus arnottiana and Pterocarpus. At lower ranks the selection ratio showed great variability with some rare species such as C.myxa, Madhuca and Lannea being highly selected. As Marsh (1981c) noted, highly selected species do not necessarily contribute greatly to the diet, nor do species fed upon extensively have necessarily high selection ratios. Although many species fed upon, both a lot and a little, had low selection ratios, there is a tendency for species with very high ratios to be fed upon a lot. The result demonstrates that the differential feeding on species evident in the annual budget was not simply a reflection of differences in tree abundances. Langurs are not taking a species diet in proportion to their availability in the environment. Variation in selection can be a result of preference (in the sense of Clutton-Brock, 1975a) and differences in item crown density and duration of availability of specific items within the canopies.

9.3.4 PHYTOPHASE SELECTION.

The species selection ratios do not, as noted above, take into account the phenology and abundance of different items. In Chapter 5 tree phenological patterns were described and an aggregate availability index for all species, for each phytophase, calculated. This provides a relative measure of item abundance but as phenology was recorded irrespective of item biomass, plant part selection cannot be compared between items. However, the aggregate index can be compared with the item feeding budgets. If, as Marsh (1981c) noted, the use of a phytophase is consistently limited by its availability a correlation between item abundance and its use would be expected. In Fig 9.12-14 the monthly availability index per item is plotted against its contribution to the diet (from Table 9.A). No relationship was evident for young leaf or leaf bud. For mature leaf there is evidence of a curvi-linear relationship. Feeding on this item tended to decline in the few months of leaf fall when availability was low. A significant linear relationship was found for fruit (r_s=0.751,p<0.01), open leaf buds (r_s=0.830,p<0.01), flowerbuds (r_s=0.626,p<0.05), and flowers (r_s=0.839,p<0.01). These items, the second, third, fourth and sixth item ranks in the annual budget respectively, were only briefly available and were consistently selected for.

The availability and utilization of species-specific items can also be compared (Fig 9.15-16). Ephemeral items, with high species selection ratios, such as Syzygium fruits, were used heavily during their brief period of availability. Some items, present throughout most of the year, such as Pterocarpus mature leaf, were only utilized during a few of those months. Others, such as Mallotus open leaf buds, available in small amounts throughout the year, were used in rough proportion to their abundance. The pattern for figs was less clear, availability and use for Ficus arnottiana and F.infectoria appeared to be unrelated. There is a suggestion in Fig 9.16 that the largest peak in utilization followed the maximum availability.

9.4 FEEDING BUDGETS : DISCUSSION.

In this discussion some aspects of langur foraging will be considered and compared with other populations of langurs and colobines. Gum and invertebrate foraging and drinking are considered in the succeeding sections of this chapter. Feeding ecology is discussed here in isolation and will be integrated with other aspects such as activity, vegetation and ranging in Chapter 10.

Hanuman langurs, along with other colobines, are generally refered to as leaf eaters or folivores. However, as Hrdy (1977b) pointed out this may be rather a misleading, but convenient, epithet. Of the colobines, P.entellus has probably the broadest diet, taking a considerable proportion of folivorous items but also fruit, flowers, gum and invertebrates. The epithet is particulary inappropriate for the hot weather months when foliar items are a minor component of the diet. Also the measurement of feeding time probably underestimates the importance of fruit in the diet (Hladik 1977). A folivore categorization may be appropriate for colobines such as C.quereza and P.senex but, if a phrase is to be used to classify diets, folivore-frugivore may be more appropriate for this langur species. The approach of Clutton-Brock & Harvey (1977), in listing species on a continuum by the percentage of foliage in the diet, is more realistic than categorization into gross diet type.

The cellulytic gut flora appears to permit, but not require, langurs to feed on mature foliage. Although apparently a very specialised adaptation, it seems to be flexible and facultative, not requiring dietary specialization, unlike true ruminants. Little information is available on the interactions between diet and microbe and colobine physiology. It may be interesting to investigate the consequences of a high invertebrate intake on the symbiosis and how the digestive specializations are reconciled with a highly diverse diet in langurs. It is not clear why Kanha langurs should be so insectivorous in comparison to other populations. It may reflect larger abundances of high density, immobile insects than at other sites. Alternatively, the difference may an artefact resulting from reduced observation time during the monsoon when invertebrates are abundant but fieldwork is difficult. The rather gradual change in item diet through the year gives the impression of seasonality and of linkage to forest phenology. Suggestions of seasonality are rather presumptive on only a year's data but evidence, not presented here, from 1980 and early 1981 suggest that monthly budgets were consistent between years. A very few species, such as Shorea, Saccopetalum, Lannea, were consistently important as food sources during many months. This pattern is a consequence of langurs feeding on a variety of items which occur at different seasons on the same species or on gum which is available throughout the year. Most species, such as Syzygium, Anogeissus, Emblica, were important for only a brief run of months, resulting from feeding on one or a few items per species which show synchronous phenology and are hence available for only a restricted time span. Marsh (1981c), Struhsaker (1975) and Oates (1977a) found similar patterns of phytophase availabilty and use to those described here. If, as is generally assumed (Clutton-Brock 1977b, Marsh 1981c) mature leaves are not 'preferred' items, owing to leaf chemistry, the reduction in mature leaf feeding below an availabilty index of about 300 may reflect the increased abundance of alternative items during and after leaf fall and not mature leaf abundance per se. Langurs generally utilized mature leaf for only a part of the period it was available, perhaps as a result of changes within the leaves, alternative forage items or in the animals' requirements. As leaf fall and reproduction tended to occur during the same season, mature leaves were the only item available in abundance for much of the year. The availabilty of the more ephemeral open leaf buds, flowers, fruits and flowerbuds was closely related to utilization, suggesting that their consumption was limited by abundance in the environment. This is evidence that these items are disproportionatly selected for and are probably preferred items.

A set of information was collected, not presented here, consisting of flow diagrams representing the mechanical actions langurs use in manipulating and processing food items. These observations revealed a great diversity of feeding techniques and a high degree of selection of parts within items. Such fine selection probably has profound consequences for nutrition, which would not be apparent in the gross scale of dietary investigations such as this. For example, langurs feeding on Pterocarpus mature leaves, the top ranking specific item, commonly masticated 3 or 4 leaves per bout before ejecting a fibre wad. All Pterocarpus trees in the study area had a large accumulation of wads below the canopy. By this technique langurs presumably ingest the leaf juices and cells whilst rejecting the fibrous material. Similarly langurs, when feeding on the large mature leaves of Bauhinia retusa, would commonly rip portions of blade from between the digitate veins. During the monsoon and cold weather langurs frequently fed on the petioles of mature leaves, discarding the blade. This was particulary prevalent for Terminalia species, the forest floor below these trees being characteristically carpeted with rejected blades. Nagel & Lohri (1973) working in the same forest calculated that for a Terminalia species, petioles constituted only 5.3 % of the entire leaf fresh weight, which could be 20 g. Langurs took great care in the manipulation of Sterculia fruits which are covered in myriads of loose urticating hairs. The fruits are terminal and langurs were occasionally seen to reach them by progressing quadrupedally, with the body swung below the branch (see Plate 12). Langurs were also seen to select between specific items, for example while feeding on the flowers of B.vahlii they only fed on white flowers and never the slightly aged yellow blossoms. In contrast, when feeding on the enormous quantities of Shorea flowers available in March, no selection was apparent and considerable amounts of peduncle were also ingested.

Recently, much effort has been expended trying to understand what aspects of leaf chemistry determines diet selection. As Chivers (1977) noted, it is not the botanical classification of food plants which is important but what trees contain in the way of beneficial and deleterious chemicals. In recent primate studies it has been suggested that it is not only primary compounds (nutrients and structural carbohydrate) which are important in diet selection but also secondary compounds, which may be harmful to the forager (Montgomery 1978, Oates et al 1980). Although these types of leaf chemicals have been implicated as important in food choice there is little firm evidence from field studies (Clutton-Brock 1977b). The nutrient levels in items will undoubtedbly play an important part in choice and trees may defend themselves by reducing nutrient levels in foliage (Hladik 1977). Oates et al (1980) investigated food selection and leaf chemsitry in Presbytis johnii in south India and found that the most heavily used mature leaves were characterized by relatively low fibre and high digestibility. They suggested that plant structural carbohydrate such as the lignin and cellulose in the cell walls were important. Milton (1980) suggested that protein and fibre content were the most important determinants of food choice in howler monkeys (Alouatta). Secondary compounds, such as alkaloids and tannins, may be produced by plants as deterrents to animal feeding (Freeland & Janzen 1974). Tannins may have a deleterious effect by precipitating food protein and digestive enzymes. Raemakers et al (1980) suggested that chemical defences tend to be more prevalent in mature versus young foliage, climax versus colonizing species, evergreen versus deciduous species and tree versus vine growth forms. However, ingestion of secondary compounds may not be universally deleterious; they may have beneficial effects by inhibiting 'bloat' and inactiviting other allelochemics (Oates 1977a). Janzen (1978) suggested that secondary compounds may be ingested as purges to eliminate intestinal parasites. Their presence may help to explain some dietetic diversity, if a varied diet results in acquiring doses of different toxins which are small enough to be neutralized (Clutton-Brock 1977b). Primates may also utilize a diverse diet in order to maintain enzymatic pathways for detoxifying a wide range of chemicals, in case large quantities of toxins have to be consumed (Rudran 1978). However, are these factors important in food selection in the field ? McKey (1978) suggested that owing to poor sandy soils, trees of a Cameroon rainforest invested more than elsewhere in predator defence, as leaf replacement involved greater expense than at nutrient rich sites. As a consequence of bristling leaf chemical defenses black colobus (C.satanas) in the forest consumed unusually large quantities of seeds for a colobine and showed greater folivorous selectivity (see Table 9.F). However, screening of tropical trees for secondary compounds suggests that they are by no means omnipresent in large quantities (Hladik 1977). Secondary compounds may be less effective against colobines than cercopithecines owing to the formers' probable ability to detoxify compounds in the forestomach microflora (Oates et al 1980).

The data from Kanha shed little light on the primary-secondary compound debate, as vegetation samples have not been analysed. However, a few aspects of their natural history are relevant. Langurs were conspicuous in their complete avoidance of some items such as mature Shorea leaves, probably the most abundant item in the forest; a mature tree can hold some 30,000 leaves (Suri 1968). This species was distinguished from the rest of the vegetation by being a climax, semi-evergreen tree and it may, by reference to Raemakers et al (1980) suggestion, be rich in secondary compounds. Similarly, the leaves of Diospyros were completely avoided. The leaves of this genus are well known for being poisonous to many folivores, perhaps because of their high naphthaquinone content (McKey 1978). Langurs consumed virtually all species of abundant fleshy fruit available. However, the complete avoidance of Casearia tomentosa fruits was notable. These fruits are regarded as poisonous by the local Baiga and used as a fish poison. The Leguminosae generally have relatively high leaf protein contents (Hladik 1977) and it is interesting that the top two species ranks for mature leaves belong to this family (see Table 9.B). Although I have no data from Kanha, young foliage usually has higher protein levels, but lower fibre and secondary compounds concentrations than mature leaves (Hladik 1977). This may explain the tendency to feed on young leaves and buds in preference to mature leaves when both are concurrently available. The selection of petioles from mature leaves and rejection of laminae may have as its cause the high concentration of vascular bundles and sap within petioles relative to lamina.

The feeding technique, whatever the determinants of food choice, is highly selective and with accidental dropping and violent canopy movements (especially adult male displays) results in a considerable fall of arboreal vegetation. From the DROP follows, in which all green matter dropped by "C" was collected and weighed, it was calculated that "C" troop dropped about 1500 kg of arboreal foliage a year. Such highly selective langur feeding has important consequences for obligate terrestrial herbivores. Vertebrates, especially chital, whose spectrum of dietary items includes forage rejected by langurs, frequently utilize this 'manna from heaven'. Langur rejects are also consumed by invertebrates such as the omnipresent beetle Gonocephalum sp. (Tenebrionidae). Nymphs of the bug Leptocoris augur (Serenthinae) appear to be dependent on langurs to make the mucus within hard Schleichera fruits available to them (Newton in press). Apart from Ficus species, langurs probably contribute little to seed dispersal directly through the deposition of their faeces. The only non-Ficus seeds found in langur dung were one example each of Saccopetalum and Cassia. Langurs were important vectors for the dispersal of Cordia myxa and C.latifolia fruits from which they rejected the mucus-coated kernels. The kernels frequently became glued to their fur by mucus and were carried long distances before being groomed out. Another important langur influence on plant dispersal was probably the dropping of viable fruits to the forest floor, where they were gleaned by jackals (Canis aureus), an omnivore without the dentition or specialized gut necessary to destroy seeds. The germinating seeds of Syzygium were frequently observed in the early monsoon sprouting from jackal faeces. Langurs may therefore be important plant dispersers, but by proxy.

The consumption of earth by langurs and other colobines has frequently been remarked upon (Ripley 1970, Roonwal & Mohnot 1977, Hladik 1977, Oates 1978, McCann 1933). Kanha langurs fed mostly on termite or termite-reworked soil, reaching a maximum of 3.0 % of feeding time in August. A reasonable supposition would be that geophagy was related to mineral nutrition. However, Hladik (1977) and Hladik & Guegen (1974) compared the mineral composition of termite mound earth with that of the diet of Singalese entellus and found that the earth had low mineral levels in comparison to foliage. They suggested an alternative hypothesis: that the function of geophagy is to absorb secondary compounds such as tannins, which can have a inhibitory affect on protein absorption. Oates (1978) reached a similar conclusion for geophagy in the Ugandan black and white colobus and noted that clays are used in medical practice to such an end and that tribal people eat soil with tannin-rich foods. Oates also suggested that soil may have an antacid function, buffering pH changes in the colobine forestomach. Information from Kanha provides little insight as to the function of geophagy as samples of earth have not been analysed. However, if a tannin absorption function was the case, geophagy would be predicted to be most prevalent when the diet was richest in tannins i.e. when mature leaves were the major diet item. Comparison (see Fig 9.1,9.10) suggests that the two patterns are not related; however as the test is based on feeding time, and not mass ingested, a relationship is not disproved.

Langurs probably suffer little interspecific feeding competition as there are few other arboreal herbivores. Avian frugivores are unlikely to be important competitors. Parakeets (Psittacula spp.), Bengal green pigeons (Treron phoenicophera) and hornbills (Tockus, Anthracoceros) range over considerably larger areas than langurs and occur at a lower biomass. The alterations of forest structure by Baiga bewar and forestry operations may have changed langur diet. The felling of Pterocarpus trees in the past (see Chapter 5) may in particular have affected langurs owing to this species' high selection ratio. The felling of B.retusa, F.arnottiana and Ehretia, all highly selected species, would be predicted to have a substantial effect on feeding ecology. Such information may be of use in the future, if commercial working plans are drawn up with an aim of minimizing the effect of selective logging on langurs.

Langur-vegetation interactions are difficult to quantify. In the late monsoon two species, Emblica and Anogeissus, clumped around Kuloo chattan were noticeably defoliated of mature leaves. Langurs fed extensively on these specific items, with a high selection ratio, and appeared to be responsible for their denudation. Other species in which langurs appear to have a significant effect on leaf density were Pterocarpus, Bauhinia retusa, F.tomentosa and Sterculia. Langurs probably considerably reduced flowers on Madhuca, Ehretia, B.vahlii, Butea, Bombax and fruit of Saccopetalum, Emblica, Lannea, Cordia, Bombax and Schleichera. It was noted in 9.3.2 that Mallotus open leaf bud was consumed throughout the year. I gained the impression that langurs were, by this regular cropping, stimulating bud production and maintaining the bushes in perpetual flush. Such pruning is similar to the suggestion that white-faced monkeys (Cebus capucinus) in Panama effectively 'prune' Gustavia trees, removing apical dominance, thereby increasing branching and the amount of foliage available (Oppenheimer & Lang 1969).

From October to February "C" troop langurs fed extensively on the pink open leaf buds of Shorea in a patch of sal forest centred on Q 17/16. The trees were, in contrast to the surrounding conspecifics, largely bare of mature leaves. The trees of this patch appeared to have renewed leaves in March, in synchrony with other sals, but then lost their mature leaves in mid-monsoon. The skeletal trees were dotted with holes, perhaps bored by cerambycid beetles, some 5mm in diameter spouting sawdust and 'ral' resin. The sals may have aseasonally shed their leaves in response to the stress of being bored into or perhaps previously defoliated trees were more susceptible to attack. Whatever the cause, langurs fed extensively on these few flushing trees and perhaps, as with Mallotus, facilitated prolonged budding. Langurs were not observed to feed on Shorea immature foliage during March leaf fall. This difference is perhaps related to variation in leaf chemistry, animal requirements and/or the alternative food available.

Is there a period of the year in which the langurs experience a food shortage ? Hrdy (1977b) suspected that the dry season at Mount Abu was occasionally a time of serious food shortage. At this time the habitat was dessicated, food choice limited, foraging more difficult and intra-specific feeding displacements frequent. Hladik (1977) found that P.entellus ate about half of the fruit production of those species consumed. For P.senex the potential food supply was gauged to be about ten times what which was actually eaten. Hladik (1977) considered that the supplies of potential food within the troop's range was often not greatly in excess of animals requirements. Milton's (1980) investigation of the mantled howler monkey (Alouatta palliata) suggested that at times they lived on narrow margins with respect to both nitrogen and energy balance. When the proportion of fruit available and consumed was low the howlers were less active than 'usual', perhaps as a consequence of problems in maintaining energy balance (Milton (1980). However, Coelho et al (1977) estimated that the energy supply available to Guatemalan howler monkeys was some 170 times the population requirements throughout the year. Although chemical analysis of Kanha vegetation has not been carried out, other work (Hladik 1977, Milton 1980) suggests generalizations as to the chemical constituents of items. Fruits tend to be low in protein and rich in non-structural carbohydrate. Leaves tend to be high in protein (especially in young leaves) but low in non-structural carbohydrate. If these generalizations hold for Kanha, it is likely that langurs have an energy rich diet in the hot weather and a more proteinaceous diet in the monsoon and winter. It is possible that langurs have a problem in maintaining a protein balance in May and June and an energy balance in November and December. There is probably an inverse relationship between food quality and quantity through the year; a diet of flush and reproductive items may be energetically rich but the food supply is probably sparse and dispersed. In contrast, with a diet of mature leaves, energetically poor, the food supply may be dense and widespread (Clutton-Brock 1975a). However, information on energy and protein budgets, the composition of food items and on animal requirements are required before a period of food shortage can be objectively identified.

That langurs have a generalist diet, broader than other colobines, has been recognised at all study sites, as summarized by Roonwal & Mohnot(1977) and Oppenheimer (1977). Of the many publications on the Hanuman only two consider feeding ecology quantitatively and in detail over an annual cycle. Oppenheimer (1978) using scans, estimated the diet of village-dwelling langurs in Bengal in terms of time spent feeding. Hladik (1977), with excellent observation conditions, measured directly the quantity of food ingested by Singalese langurs in semi-deciduous forest. Both studies spanned an annual cycle. The food items consumed, in broad categories are tabulated below :

Study site	**Leaf**	**Flower**	**Fruit**	**Source**
Kanha	51.7	9.5	24.5	this study
Singur	54	5	37	Oppenheimer (1978)
Polonnaruwa	48	7	45	Hladik (1977)

Oppenheimer (1978) found a diet similar in structure, in terms of items, to Kanha but of quite different species composition. The top 10 ranking species made up 66 % of feeding time whilst in Kanha the top 12 species contributed 70 %. During 19 months of the Singur study 69 species were fed upon, as opposed to 60 at Kanha. Some of the food plants at Singur were probably introduced and cultivated. The seasonal variation in item feeding time also followed a similar pattern to Kanha. Flowers were only consumed prolifically in February and March whilst fruit consumption remained at a high level throughout the year with a peak in May and, unlike Kanha, a peak in December. Leaf consumption was highest in the monsoon and early winter and lowest during periods of heavy feeding on reproductive items. Comparison of diets across two years suggested that some of the diet seasonality was dependent on the timing of the break of the monsoon.

Hladik (1977) compared ingestion diets of P.senex and the Hanuman living in the same forest. He was able to show that differences between time spent feeding on items and the quantity of food ingested were small for P.senex but large for P.entellus. For example, there was a ten fold difference between the two measures for flowers and leaf buds. However, the annual diet was, in terms of ingestion, similar to that for Kanha and Singur using feeding time. At Polonnaruwa, which shared some tree species with Kanha, the top 10 ranking species accounted for 70 % of the diet. Interestingly, the eighth rank at Polonnaruwa was Cassia fistula, a species abundant at Kanha but rarely fed upon, apart from the occasional insect or seed. Also in Ceylon, Schleichera oleosa was the third rank and Adina cordifolia fourth, whereas at Kanha the former was rank 31 and the latter was never observed to be fed upon. Although, both species are probably rarer in Kanha than in Ceylon, both had substantial biomass (see Chapter 5). The dietary seasonal variation in Ceylon was also similar to that in Bengal and Kanha, with a tendency to be frugivorous during the two dry seasons and folivorous during the rainy season. Therefore, the three studies of the Hanuman suggest that whilst a foliviore, fruit is a very important dietary component and predominates during the hot season.

Although the Hanuman langur has a relatively broad frugivorous diet for a colobine, in comparison to the cercopithecines it has a very leafy diet. A summary of feeding budgets of a variety of cercopithecids, abstracted from field studies similar to this one in methodology, is given in Table 9.F. There is a striking contrast between the diets of the two sub-families: the colobines feed predominantly on leaves plus some fruit and flowers but rarely insects, whilst the cercopithecines are predominantely frugivores and insectivores. This distinction probably reflects the digestive specializations of colobines, permitting feeding on abundant, but poor quality, food (Struhsaker 1975,Clutton-Brock 1977a). Among the colobines, P.melalophos and C.satanas are the most frugivorous. The reasons suggested for the high seed intake in the latter species are discussed above. The most folivorous species are C.guereza, P.senex and P.obscura. The diet of Kanha langurs was similar to that of P.johnii at Kakachi, apart from the latters greater investment in feeding on young leaves and less on mature leaves (Oates et al 1980). The avoidance of mature leaves may be explicable by the evergreen nature of the johnii habitat, which may therefore contain higher levels of secondary compounds than found in Kanha foliage. As in Kanha, johnii fed on large quantities of mature leaves, but from a very few tree species. In both studies, one species providing mature leaves (Pterocarpus in Kanha, Gomphandra in Kakachi) was the single most important species-specific item in the annual budget and both showed high selection ratios (Oates et al 1980).

Unlike red colobus at Gombe and Kibale and black and white colobus at Kibale (Struhsaker 1975,Oates 1977a) no one species was a staple across the year for Kanha langurs. No species was important in all months but Shorea was important in many months. Its use declined when only mature leaves were available. The differences between Kanha and the East African sites may in part be due the greater seasonality at the Indian site; the phytophase synchrony between and within species means that no one species bears preferred items throughout the year. In commonly feeding on four of the seven major plant parts from each species, langurs probably utilized most of the species-specific items available. In contrast, Waser (1977a) found that mangabeys generally selected only a single plant part from each tree species. Langur dietetic diversity was high, H' for the annual diet being 3.157, in comparison to 2.651 and 2.962 for two red colobus populations (Struhsaker 1975) and 2.08 for black and white colobus (Oates 1977a).

Hladik (1977) was able to compare the ingestion diets of P.senex and entellus living in the same forest. The senex diet was of low diversity, seasonally feeding on 80 % mature leaves and low proportions of fibrous fruits. In contrast, the *entellus* diet was highly diverse, never feeding on more than 50 % mature foliage but seasonally consuming up to 90 % fleshy fruit. Ten tree species in *entellus* and three in *senex* accounted for 70 % of food ingested. Hladik (1977) and Clutton-Brock (1974a) suggested that this pair of species may be ecological analogues of the African *C.badius* and *C.guereza* which show similar dietary differences linked to variation in ranging and social organisation (see Chapter 10).

Therefore, in conclusion Hanuman langurs have one of the broadest of colobine diets, feeding extensively on both foliar and reproductive items with some gum and invertebrates. With the temporal co-incidence of leaf fall and tree reproduction, mature leaves constitute the only abundant available food for much of the year. The facultative digestive specialization allows them to cope with this resource, permitting occupation, like black and white colobus (Clutton-Brock 1974a) of very seasonal forests.

9.5 GUMMIVORY.

9.5.1 GUM FEEDING : OBSERVATIONS.

Gums, one of the three major categories of plant exudate, are amorphous acidic polysaccharides. They are entirely soluble in water or form a mucilage. Their physiological function to the tree is probably to seal wounds against infection, analogous to mammalian scab formation. Gum is distinct from sap, the fluids carried in xylem and phloem, and resins which are water insoluble, acidic phenol or terpene derivatives (Bearder & Martin 1980).

Langurs of "C" troop were observed to feed on tree gum and, as it is an unusual colobine food, its consumption is considered in some detail in this section. Gum feeding was measured both in terms of percentage of time spent feeding from scan samples and as the number of opportunistic observations of langurs feeding during the seven days of DROP and SCAN 'follows' per month. Seasonal variation in the two patterns are very similar (see Fig 9.10) and in this section the latter measure has been used because of the larger sample size. If a langur fed at a gum site and returned to feed again within one hour it was regarded as one feeding bout. If the animal returned after an hour or visited a different gum tree two bouts were recorded.

Langurs of "C" were observed to feed on gum from ten species of tree (61 individuals) as listed in Table 9.E. Only one observation was made of langurs feeding on sal 'rall' resin, despite its abundance in the study area. In addition, in Ocober 1981 langurs were observed to feed on 'lac', the excretions of a coccid inscect (Carteria lacca) feeding on Butea monosperma (Cotes 1893). Lac is similar in appearance, and perhaps also chemically, to resin (Ford-Robertson 1971). Variation in the number of observations of gum feeding per month is shown in Fig 9.17 for each species of tree utilized.

To compare the frequency of gum feeding with its availability, the quantity of gum present in a sample of 17 gum producing trees at which langurs were seen to feed, were monitored at the end of every month (see 3.2.1; Bearder & Martin 1980). The gum sites were inspected and the colour and morphology of gum flow described. The quantity of gum present at the site was noted on a 1-4 index in the same manner as used in monitoring tree phenology (see 5.2). This index of availability is plotted for each species in Fig 9.17. Most gum issued from damage which penetrated the bark. A sketch of the most frequently utilized species, Lannea, is given in Fig 9.18 to illustrate the types of gum sources. On occasions the flow of gum out of Lannea clefts was rapid enough to be visible.

Terminalia gum sites were on terminal twigs and the cause of production was not ascertained. Sterculia produced thin twists of gum from 'pores' in the bark and occasionally from branch-loss stumps. Most of the Cordia latifolia gum production was the the result of axe wounds delivered by Baiga tribal people in the course of cutting fire making sticks ('gursa') or bark for rope. The tribal habit of blazing trees caused gum flow from Lannea, Anogeissus and Buchanania. Gum also issued from damage to an Anogeissus bole, caused by deer (probably Axis) scouring into the bark with antler tips. The greatest variety of gum sites was found on Lannea. Elephants debarked the bole and woodpeckers (probably Chrysocoloptes festivus and/or Dinopium benghalensie), in drilling into the trunk, caused considerable gum flow. Wood-boring invertebrates, such as cerambycids, may also have induced gum production (Bearder & Martin 1980). The major source of Lannea gum was from clefts or rents in the bark often surrounding dead wood and perhaps resulting from branch-loss. Also in Lannea the junction of primary and secondary branches appeared to be common gum sites. During the hot weather months of May and early June many Lagerstroemia plants, especially small trees some 6' high, glistened with droplets of a gum-like substance dripping from leaf tips. Tasting very sweet and sticky to touch the exudate crystallised into a white amorphous powder coating the leaves. This behaviour is not recorded by Brandis (1878, 1906) or Witt (1916) but was known to the local Baiga who ate the gum (Mungal pers.comm.). On one occasion each in May and June a juvenile langur was seen to feed extensively on this exudate, placing the leaf tips in its mouth and removing the gum.

The frequency with which "C" troop fed at different categories of sites and species is shown in Tab 9.E. The frequency of troop gum feeding over the entire year was 0.45 observations/day. I could not detect any preferences for particular colours or consistences of gum issuing from sites. Both crystalline hard and mucilaginous gum were consumed, usually taken direct by mouth, although occasionally pieces were picked by hand and transferred to the mouth. The only observation of a langur digging was of an adult female, which removed soil at the base of a Anogeissus bole, with fingers, to uncover a partially subterranean gum deposit.

The comparison of plots of gum feeding frequency and gum availability does not reveal any clear relationship between them, apart for Lannea. In this species the two patterns are similar, except for an April peak in feeding not apparent in the availability score. Lannea was the most frequently utilized species with the largest number of individuals trees fed upon. The majority of gum feeding occurred on or about the chattans with Lannea, Sterculia, Buchanania and Anogeissus tending to be clumped about these rocky areas (see Chapter 5). Little gum feeding was observed in the surrounding sal forest or on the meadows.

The most frequently used gum sites were those at major natural damage (46.7 %) with minor damage, pore sites and those of unkown origin contributing 28.0 %. Feeding at animal induced sites contributed only 5.4 %. Gum contributed 1 % of feeding time in the annual budget but this probably underestimates its importance as considerable quantities could be consumed in one brief sitting. At cleft and bole sites especially langurs appeared to induce considerable gum flow by gnawing at the actual site of issue. This was probably particularly potent when done by adult males with their large canines and associated musculature.

9.5.2. GUM DISCUSSION.

Among colobines, exudate feeding has only been reported for Presbytis entellus. There appears to have been confusion over the definition of types of tree exudate and it seems likely that some of the published observations of langur 'sap' consumption are in fact gum. Ripley (1970) noted Singalese entellus feeding on 'sap' of Chloroxylon swietenia (Meliaceae), Eleodendron glaucum (Celsatraceae), Sterculia foetida and Lannea coramandelica. Starin (1978) observed Gir langurs feeding on 'sap' from T.ballerica and Acacia cathechu (Mimosaceae). Oppenheimer (1977) recorded 'sap' feeding at Singur from species of Anacardiaceae and at Jodhpur from trees of Ascelapedaceae and Leguminosae . Hrdy (1977b) observed langurs at Mount Abu feeding on the 'neera' sap of a palm (probably Borassus flabellifer L) issuing from wounds in the bark cut by local people. However, at none of these sites does plant exudate feeding appear to be as important a part of the diet as it was in Kanha.

Gum feeding has been reported as a dietary component for a wide range of primates from Galagos to chimpanzees (Pan troglodytes). Resin feeding is in contrast very rare, perhaps as a consequence of problems in digesting a water insoluble substance. Gum appears to be a major food source for several of the smaller primates belonging to the genera Cebuella, Callithrix, Galago, Euoticus, Perodicticus, Microcebus and Phaner (Coimbra-Filho & Mittermeier 1977). Some marmoset and bushbaby species appear to be specialist gumivores and have a dentition adapted for gum foraging and the induction of gum flow (Bearder & Martin 1980). The more facultative gum feeders do not show anatomical adaptation and do not generally cause gum production by biting through the bark. In these species gum feeding is more opportunistic, taking advantage of production resulting from mechanical damage or injury. Langurs in Kanha belong to the latter category of non-specialist opportunistic gumivores. They exploit gum flowing as a result of damage to trees by people, animals, mechanical injury and natural pores. Although langurs were occasionally observed to stimulate gum flow, new sites were not created.

In general, gums consist of polysaccharide carbohydrates with small quantities of fibre, protein and minerals, with when moist a consistency similar to treacle or toffee. Anderson & Hendric (1973) found that Lannea coramandelica gum was composed of 70 % galactose, 11% arabinose, 2% rhamnose and 17 % uronic acid. Anderson & Bell (1974) found a similar composition for Terminalia tomentosa. Gum from the other Kanha trees does not appear to have been analysed.

Gum is a predictable source of easily harvestable, high energy content food, probably relatively free of plant secondary compounds but low in protein. The large peak in Lannea gum consumption in April 1981 during a period of low gum availability may be related to the properties of the exudate as a quick, high energy food source. During April, "C" had numerous stressful contacts with the "Q" all-male band which resulted in infanticide, takeover and the disruption of feeding and ranging (see Chapter 6). Energy requirements may have been high owing to the highly energetic encounters between the two groups. Females with infants were unable to feed for long periods owing to their apparent hiding from the band males. Therefore, the high level of feeding on gum, a high energy, but low protein, readily harvestable food, may have been to offset dietary disruption.

As gum was largely consumed from trees in dry deciduous forest on the chattans and not in the sal forest, gum feeding may be more frequent in hill forest langurs, which have access to a larger number of gum trees. The restriction of gum trees to the chattans, with many other important food species, may make the rocky outcrops very valuable feeding sites. It may explain the central position of Kuloo chattan within the exclusive area of "C"'s range.

9.6 INSECTIVORY.

9.6.1. INVERTEBRATE FEEDING : OBSERVATIONS.

The consumption of invertebrates by "C" langurs showed pronounced seasonal variation (see Fig 9.9) with a sudden dramatic increase in the proportion of time spent feeding on this category in July and a subsequent decline during the winter. Langurs fed on only a limited range of invertebrates. As the species consumed were characteristically found at high density, it was usually relatively straightforward to identify the taxa involved and langurs spent little time searching. The major component of the annual animal diet was cercopid bug nymphs ('cuckoo-spit bugs') which were taken in July only, from the mature leaves of the following species :

Bauhinia vahlii	Emblica officinalis
Ficus arnottiana	Ficus tomentosa
Grewia tilaefolia	Lagerstroemia parviflora
Semecarpus anacardium	Stereospermum saeveolens
Tectona grandis	Terminalia tomentosa

The nymphs were ingested direct from the mature leaf by being licked off with most of the encompassing froth. A sign of recent langur cercopid feeding was a coating of this froth on their facial hair. An adult cercopid collected from amongst nymphs on F.tomentosa was identified as Tylus nebulus. Nymphal cercopids were only observed in July.

The second most important insect group were lepidopterous larvae which were also most common in the monsoon. Feeding on them was observed from July to January (excluding December). Langurs of "C" were noted to feed on caterpillars from the following tree and shrub species :

Bauhinia retusa	Cassia fistula
Diospyros melanoxylon	Flamengia semilata
Holarrhena antidysenterica	Lannea coramandelica
Ougenia dalbergioides	Saccopetalum tomentosa
Schleichera oleosa	Semecarpus anacardium
Shorea robusta	Syzygium cumini

A caterpillar collected from C.fistula, thought to be of the same species as fed on by langurs, was reared and the resulting imago was identified as a Catopsilia pomona (Pieridae). During caterpillar foraging langurs showed three characteristic behaviours :

1/ In B.retusa and C.fistula langurs occasionally sat and visually scanned the canopy, looking for larvae and turning leaves over to inspect the underside.

2/ The larvae living on Semecarpus trees bound 3-6 leaves together, forming a shelter. Langurs would frequently inspect these constructions and pull them apart to feed on the caterpillars.

3/ Some larvae would, on being disturbed by a foraging langur, wriggle violently and fall off the leaf, presumably as an escape response. Larvae on B.retusa would, on being disturbed, drop from the leaf 2-4 feet and hang motionless on a fine silken thread anchored to the leaf. Langurs were occasionally seen to defeat this strategy by hauling the larvae up by the thread, hand over hand.

It was thought likely during fieldwork that most of the unidentified invertebrates were also lepidopterous larvae. A variety of other invertebrates were also seen to be eaten. In July a juvenile female fed on two legs of a green Heteropoda species of spider. In May and June 1981 langurs were occasionally seen to feed on the scale insect Perrisopneumon ferox. This species was extensively eaten by "B" troop in

June 1980 from *Lagerstroemia* trees and the ground below. On 14 June 1980, after the emergence of alate termites from termitaria, an infant-two of "B" was seen to stand bipedally and catch, by clapping its hands together, a large flying termite which it ingested, probably after having removed the wings. At the onset of the monsoon enormous numbers of termites emerge from the ground but these swarms were not seen to be exploited by langurs. On two occasions in October 1981 langurs were seen to orally squeeze and suck at cocoons (probably of saturnids) picked from *Syzygium* canopies. Invertebrates, especially solitary Hymenoptera, were inevitably consumed while feeding on *Ficus* figs.

9.6.2. INVEREBRATE FEEDING :DISCUSSION.

Other studies have also shown that langurs occasionally eat invertebrates. For example, Yoshiba (1967) reported consumption of termites, gall larvae from *T.tomentosa* and caterpillars from *Tectona*. Oppenheimer (1978) noted ant consumption and Rahman (1974) pupae. Ripley is reported by Roonwal & Mohnot (1977) to have observed langurs feeding on spiders' webs. Gokulpura, Mehra and Krishnaswami (1963) found that langurs did considerable damage to lac crops by feeding on lac insects (*Carteria lacca*) and the encrustations they produce. In none of these studies, nor in Hladik's (1977) work, did insects have the dietary importance that they had in the early monsoon in Kanha. No other types of animal matter were observed to be eaten, apart from one occasion in which a langur gnawed a chital vertebrum. Rahman (1974) observed langurs feeding on birds eggs.

The seasonal cycle of invertebrate feeding, with the majority confined to the monsoon, probably reflects seasonal variation in insect abundance. During the hot weather insect density was low and suddenly increased with break of the monsoon. The concentration of insect feeding at the beginning of the rains probably reflects langur feeding on the early and more sedentary life history stages.

Both the major components of the animal diet, cercopid nymphs and lepidopterous larvae, occurred at high density and were easily harvested. Most of langur insectivory involved taking items from leaf surfaces and in terms of foraging behaviour was analogous to feeding on small foliar items such as leaf buds. Langur insectivory differs substantially from the behaviour shown by the more omnivorous cercopithecines, such as the mangabey, which spends considerable search and handling time in examining and pulling apart moss, epiphytes, dead wood and bark (Waser 1977a). These primates employ a more specialized strategy, qualitatively different to the approach they use when feeding on foliage. Langurs do not appear to have adopted such a strategy but feed on insects only when they occur in abundance and as if they were small plant parts.

Langurs of "C" tended to concentrate insectivory on only a relatively few trees, which is likely to have had profound consequences for the population dynamics of the insects and their relationship to their host. Langur predation on cercopids from F.tomentosa and F.arnottiana and caterpillars from B.retusa and Semecarpus was especially intensive and restricted to a few trees on which insect density was high. It seems very likely that such predation is a major influence on the population dynamics of the prey species and may reduce invertebrate defoliation on some tree species.

In a year-long study of Presbytis johnii in the Western Ghats only one instance of animal predation was seen, a stick insect (Oates et al 1980). The Malayasian P.melalophos and P.obscura apparently do not feed on invertebrates (Curtin 1980). No invertebrate food in the diet of wild P.senex appears to have been recorded (Roonwal & Mohnot 1977). Of the African colobines none appear to be as insectivorous as

P.entellus. Insectivory was not recorded in C.satanas (McKey 1978), C.guereza (Oates 1977a) or C.badius (Clutton-Brock 1975a, Marsh 1981c). However, Struhsaker (1975) found that, although actual observations of C.badius eating insects were rare, it was suspected in 'innumerable cases' but was under-estimated due to observation difficulties. Unlike langurs they did not feed on high density aggregations of invertebrates, but spent considerable time searching leaves and dead wood.

In contrast to colobines, cercopithecines such as Cercocebus albigena spent 26 % of scan records feeding on invertebrates among moss, epiphytes and dead wood, taking very few items from leaf surfaces (Waser 1977a). Rudran (1978) found that invertebrate food constituted nearly 20 % of the blue monkeys' (C.mitis) feeding time but most items were removed from leaf surfaces.

Therefore, Kanha langurs are the most insectivorous colobines studied to date. The insectivory is highly seasonal and in terms of time spent feeding, langurs take considerably less animal food than cercopithecines. Perhaps the rarity of insectivory among colobines is related to the specialized cellulytic digestive system, which may have difficulty coping with a large intake of animal protein.

9.5. DRINKING

Langurs were observed to drink water from streams, pools, concave leaves and once from a bole cistern. They drink in a crouched position, bringing lips directly to the water surface as described by Roonwal & Mohnot (1977). They were never seen to lick water from foliage or fur. Drinking was recorded opportunistically whenever observed and its frequency per day, from the 12 days of follows per month, is shown in Fig 9.19. Drinking was recorded if one or more members of "C" were seen to drink. It is very unlikely that drinking from streams was missed because of good visibility. However, drinking from small forest pools in the monsoon was probably underestimated. The results suggest that drinking was most frequent in the monsoon and least frequent during the hot weather. This seasonal variation is counter-intuitive; drinking would be expected to be more frequent in the hot, dry summer than the wet, humid monsoon. At least two factors could account for this. Firstly, the frequency of drinking may not reflect the volume of water intake. With the abundance of standing water in the monsoon, langurs may drink small quantities frequently, whilst in the hot weather they could drink large amounts infrequently. Secondly, diet may be important. The water content of items consumed in the hot weather, mainly flush and fruit, is probably considerably higher than that of the monsoon diet of mature leaves. Dietary water may therefore fulfil most requirements in the summer but not in the monsoon. It is also possible that metabolic requirements may be increased in the monsoon, if the digestion of mature leaves requires larger amounts of water than other items.

9.8 FEEDING ECOLOGY : SUMMARY.

1/ The proportion of time "C" troop spent feeding on items and species was estimated from seven days of dawn-dusk follows per month,during which the troop was scanned every half hour.

2/ In the annual diet mature leaf constituted 34.9%, young leaf 3.6%, leaf bud 2.8%, open leaf bud 7.9%,petiole 2.4%, flowerbud 6.6%, flower 2.9%, fruit 24.5%, gum 1% and invertebrates 2.8%. The food item was unrecorded in 6.8% of observations. During scans "C" fed on 53 of the 68 species of tree and climber present. The top 12 food species contributed 70% of the annual budget; Pterocarpus contributed 12.23% and Shorea 12.08%. The top species-specific item was Pterocarpus mature leaf. H' was 3.157 and 13.2% of feeding records were terrestrial. Bias, resulting from differential visibility of animals whilst feeding in different species was tested for but concluded to be unimportant.

3/ There was considerable variation between monthly feeding budgets. In the hot weather reproductive items predominated, whilst mature leaf dominated the winter diet. During the monsoon, fruit, mature leaf and invertebrates were important. Monthly statistics of diet overlap and diversity were calculated. No one species was important in all months but Shorea was important in most months.

4/ Selection ratios demonstrated that langurs did not utilize tree species in proportion to their abundance. Significant positive linear correlations were found between the monthly phytophase availability index and monthly consumption of fruit, flowers, flowerbuds and open leaf buds. A positive curvi-linear relationship was found for mature leaf.

5/ Gum was eaten from ten tree species (61 trees), from sites produced by natural mechanical and animal damage, with a frequency of 0.45 bouts/day. Lannea coramandelica was the most frequently utilized species. No clear relationship was found between gum availability and its consumption.

Langurs were concluded to be non-specialist opportunistic gummivores, occasionally stimulating gum flow but not creating new sites. The high level of gum feeding in April was suggested to be an attempt to offset the dietary disruption resulting from infanticidal attacks by "Q" band. Gum consumption was largely restricted to the mixed forest patch, emphasising the importance of chattans in feeding ecology.

6/ Insectivory, predominantly lepidopterous larvae and cercopid nymphs, mostly occurred in the monsoon. It was highest in July when insect feeding accounted for 24.9% of the budget, probably owing to the peak in abundance of immobile, immature invertebrates after the break of the monsoon. Langurs, in contrast to the more insectivorous cercopithecines, fed on insects by using similar behaviour to that employed when feeding on small plant parts and did not show specialized searching behaviour. The low level of insectivory among colobines generally may be related to their specialized digestion.

7/ Drinking frequency was higher in the monsoon than in the hot weather, perhaps because the measure does not reflect volume intake or because of dietary differences requiring higher water intake in the rains. Geophagy, mostly of termite-reworked soils was, contrary to a prediction of the tannin binding hypothesis, not associated with a high level of mature leaf in the diet.

8/ Langur digestive specializations do not appear to require a narrow diet but permit seasonal subsistence on large quantities of mature leaf. Aspects of food choice and leaf chemistry are discussed. The consequences of langur dropping of vegetation for obligate terrestial herbivores are noted. Langur-mediated plant dispersal is restricted to a few tree species and one of the most important mechanisms is probably through the 'gleaning' of dropped seeds by jackals.

9/ It is suggested that, of the tree species present, the felling of those utilized with the highest selection ratios would have the greatest effect on langur feeding. Observations suggest that langurs significantly deplete certain tree species of leaves, flowers and fruits. Langur feeding on Mallotus open leaf buds appeared to stimulate further production,maintaining the bush in perpetual flush.

10/ Although not possible to objectively identify a season of food shortage it is suggested that the hot weather diet is energetically rich but poor in protein, whilst the monsoon and winter diet is proteinaceous but energetically poor.

11/ Other Hanuman langur studies agree that whilst primarily a folivore, fruit is also important and is seasonally a prime food. This species has one of the most diverse, frugivorous and insectivorous diets of any colobine but is relatively folivorous in comparison to most cercopithecines. The absence of a year-round staple food species in Kanha langurs, in contrast to East African colobines, may result from the pronounced seasonality in central India.

FIG 9.1 MONTHLY VARIATION IN FEEDING BUDGET, BY ITEMS.
Symbols as below. N=6787

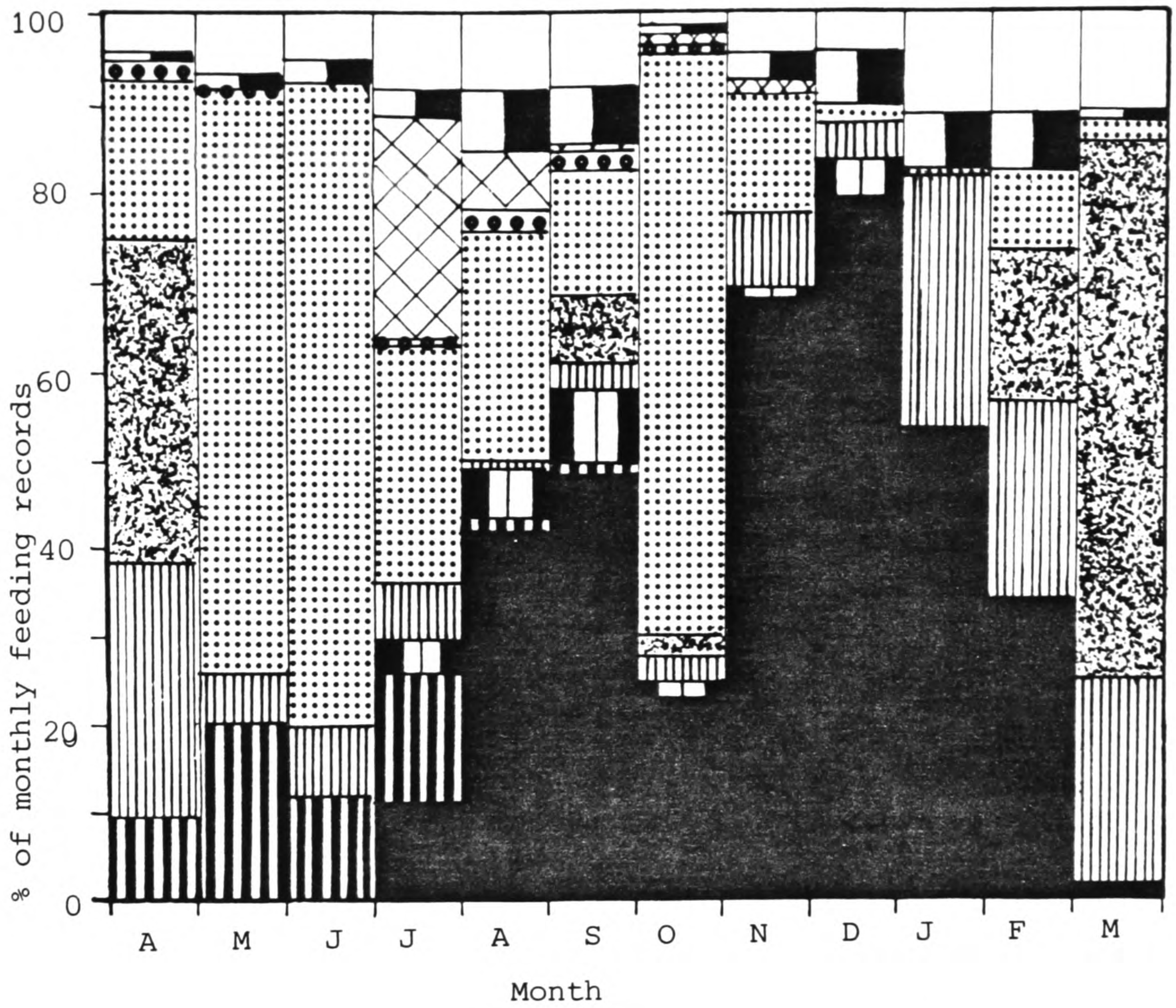


FIG 9.2 ANNUAL FEEDING BUDGET,BY ITEMS N=6787

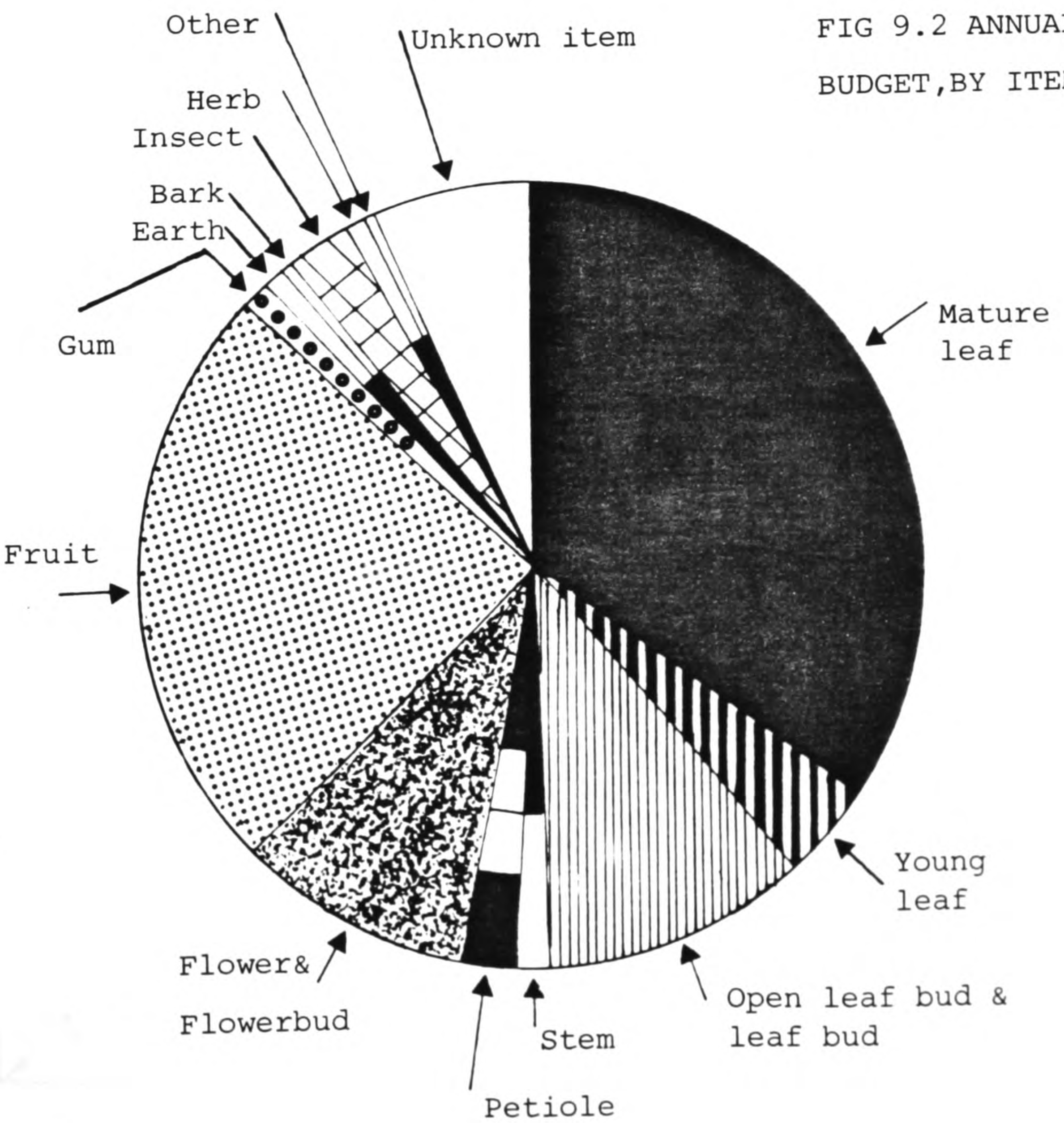
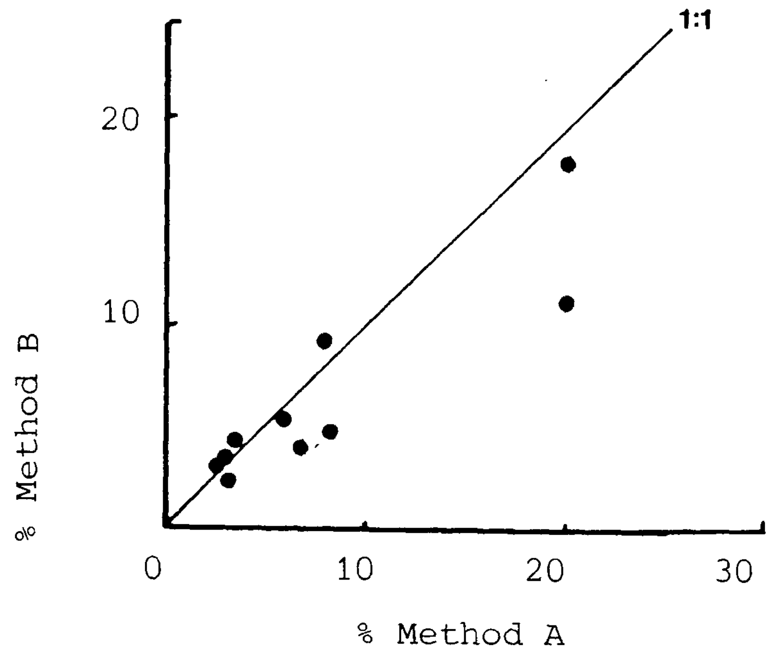
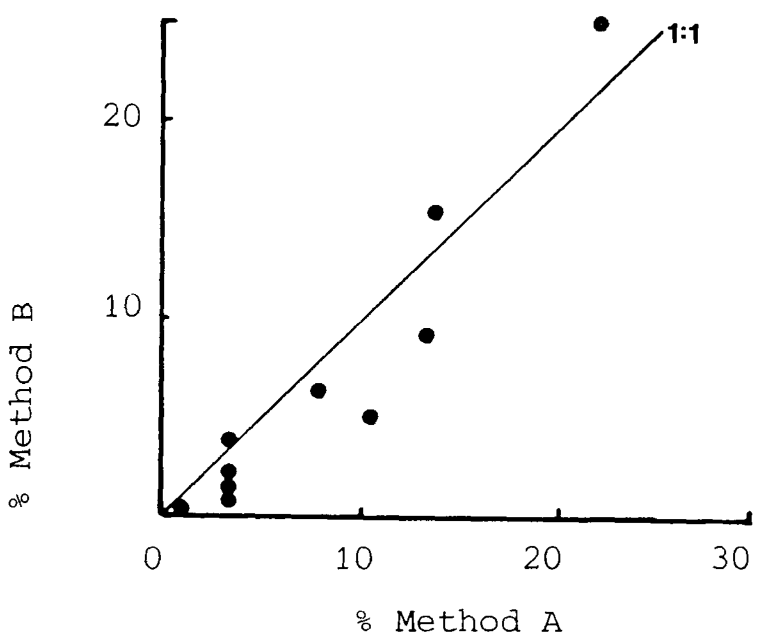


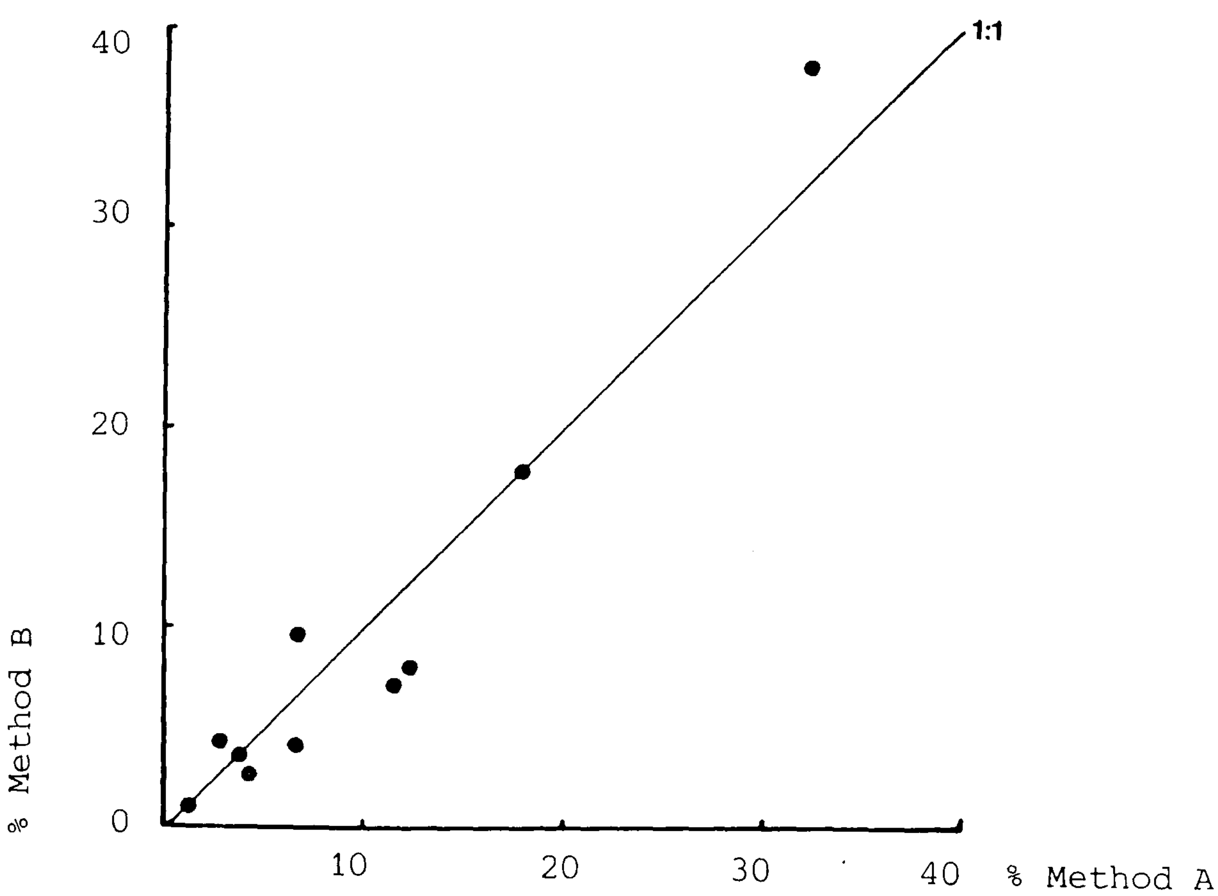
FIG 9.3 TEST FOR ASSOCIATION BETWEEN FOOD SPECIES AND VISIBILITY. For ten species most important in the diet of three months. (see text for details)



AUGUST 1981



MAY 1981



DECEMBER 1981

FIG 9.4 RATE OF INCREASE OF TREE SPECIES RECORDED AS FED UPON BY "C" TROOP WITH ACCUMULATION OF OBSERVATION TIME. April 1981-March 1982

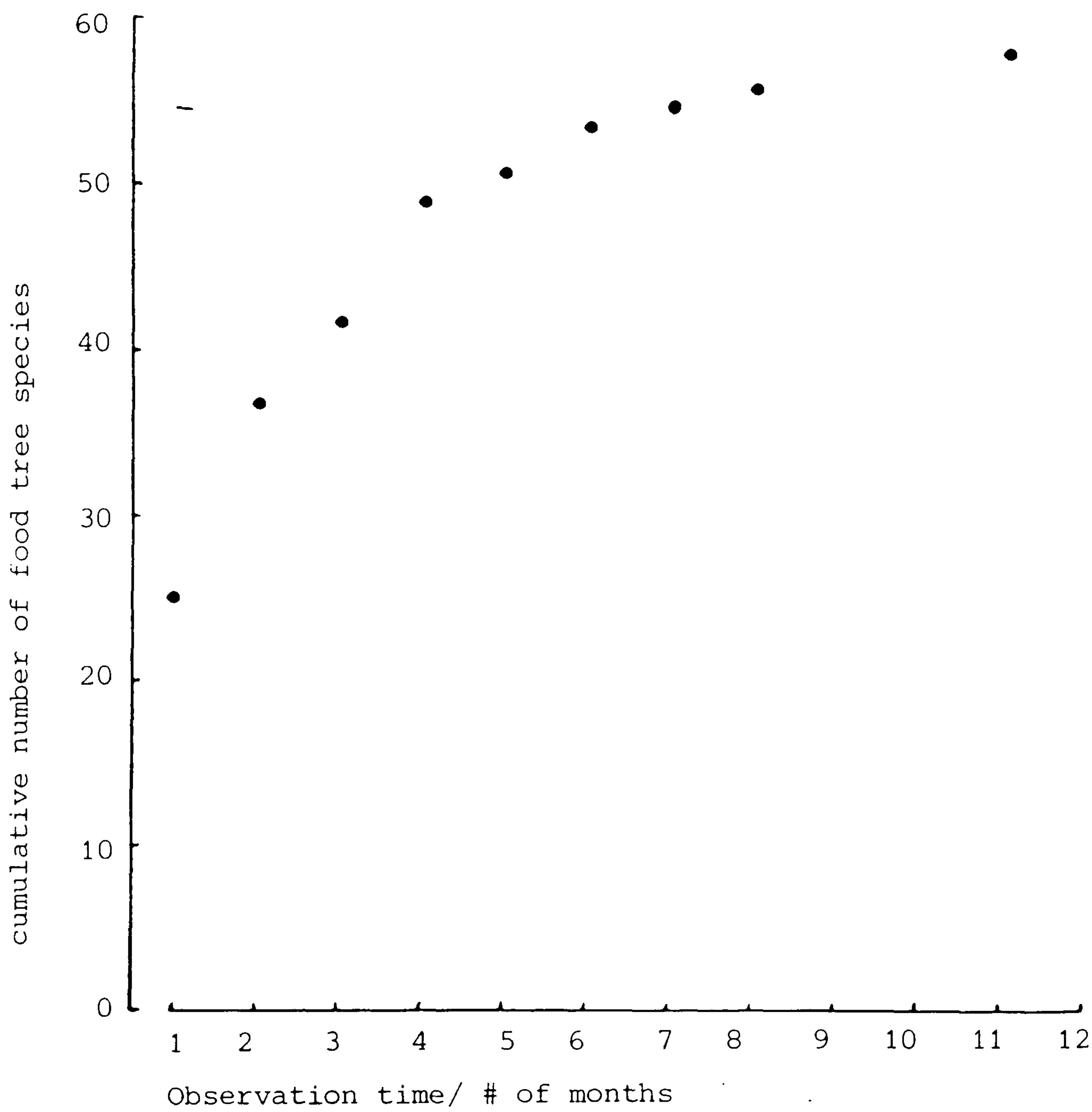


FIG 9.5 MONTHLY VARIATION IN FEEDING ON Shorea robusta items

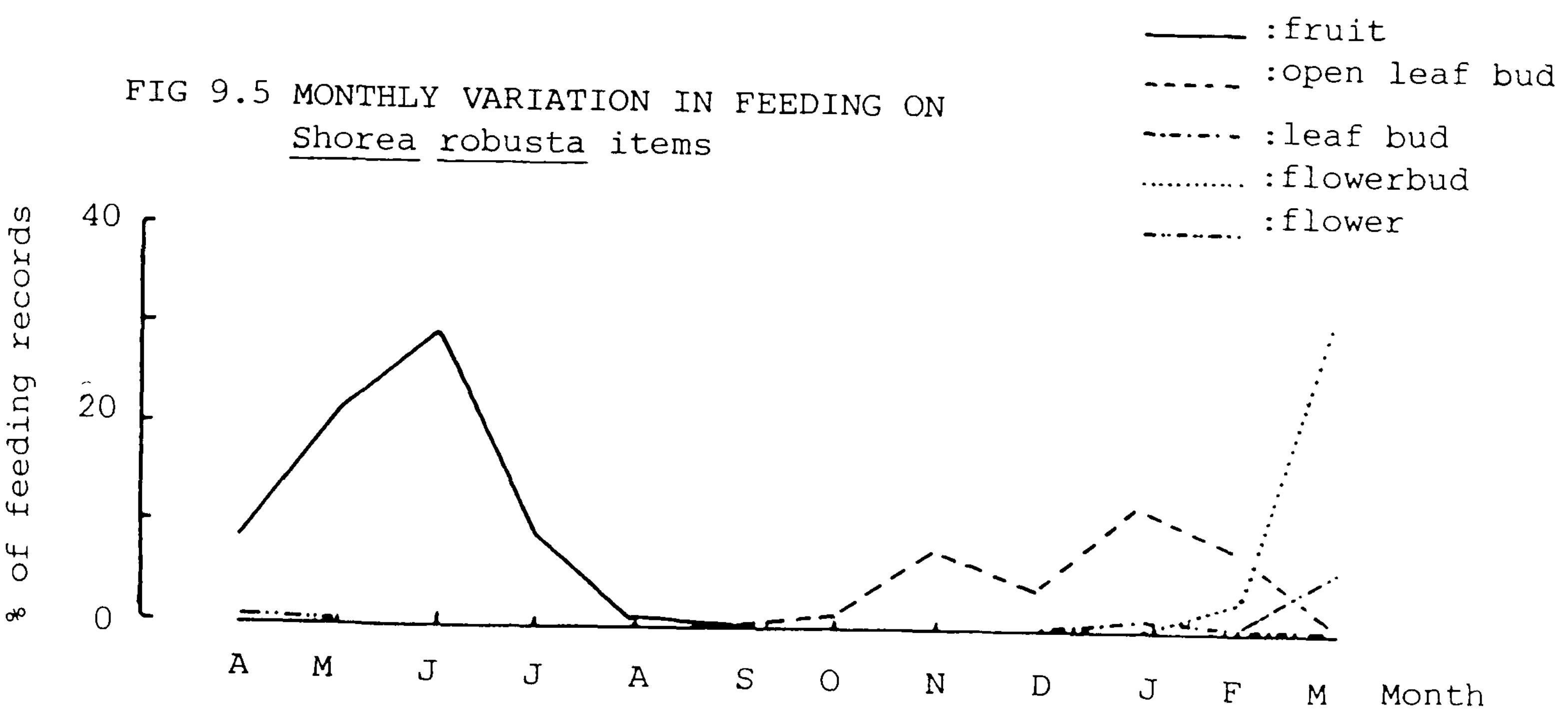


FIG 9.6 % FEEDING TIME FOR TEN MOST FED UPON SPECIES IN EACH MONTH AND FOR ANNUAL FEEDING BUDGET.

(Scale for all months as October)

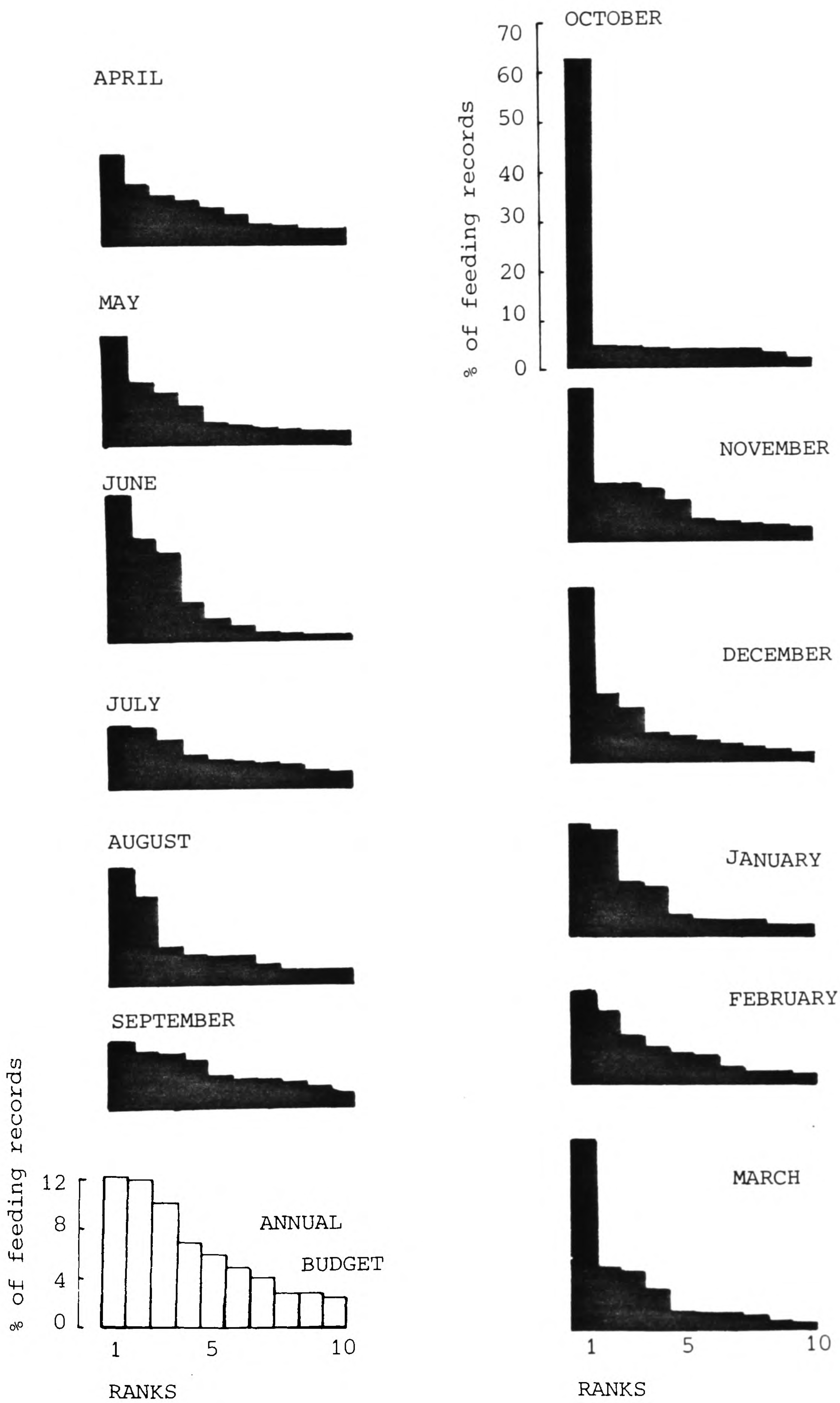


FIG 9.7 MONTHLY VARIATION IN DIET DIVERSITY (H') "C" TROOP FEEDING BUDGETS.
April 1981-March 1982. Items and species specific items.

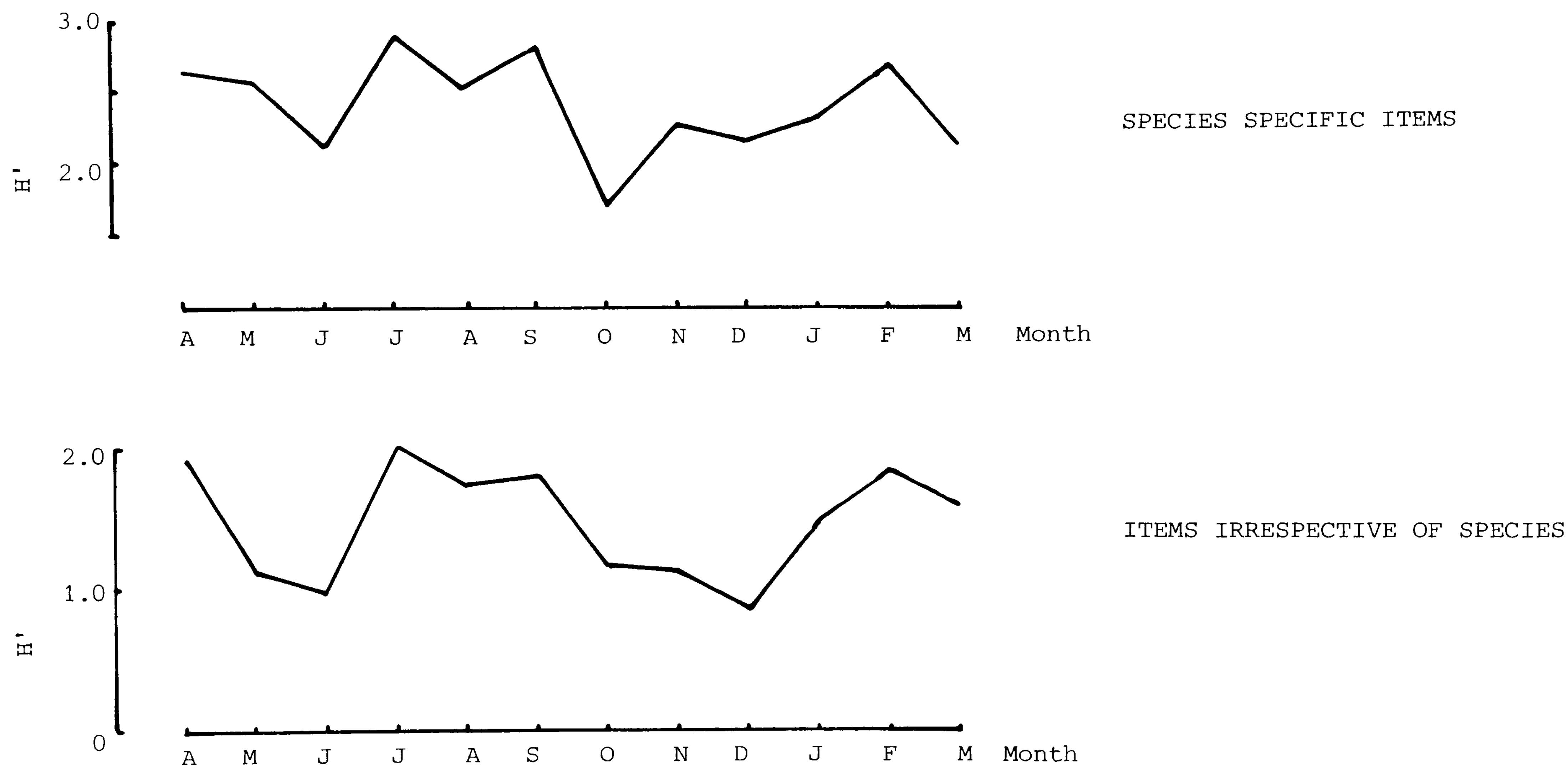
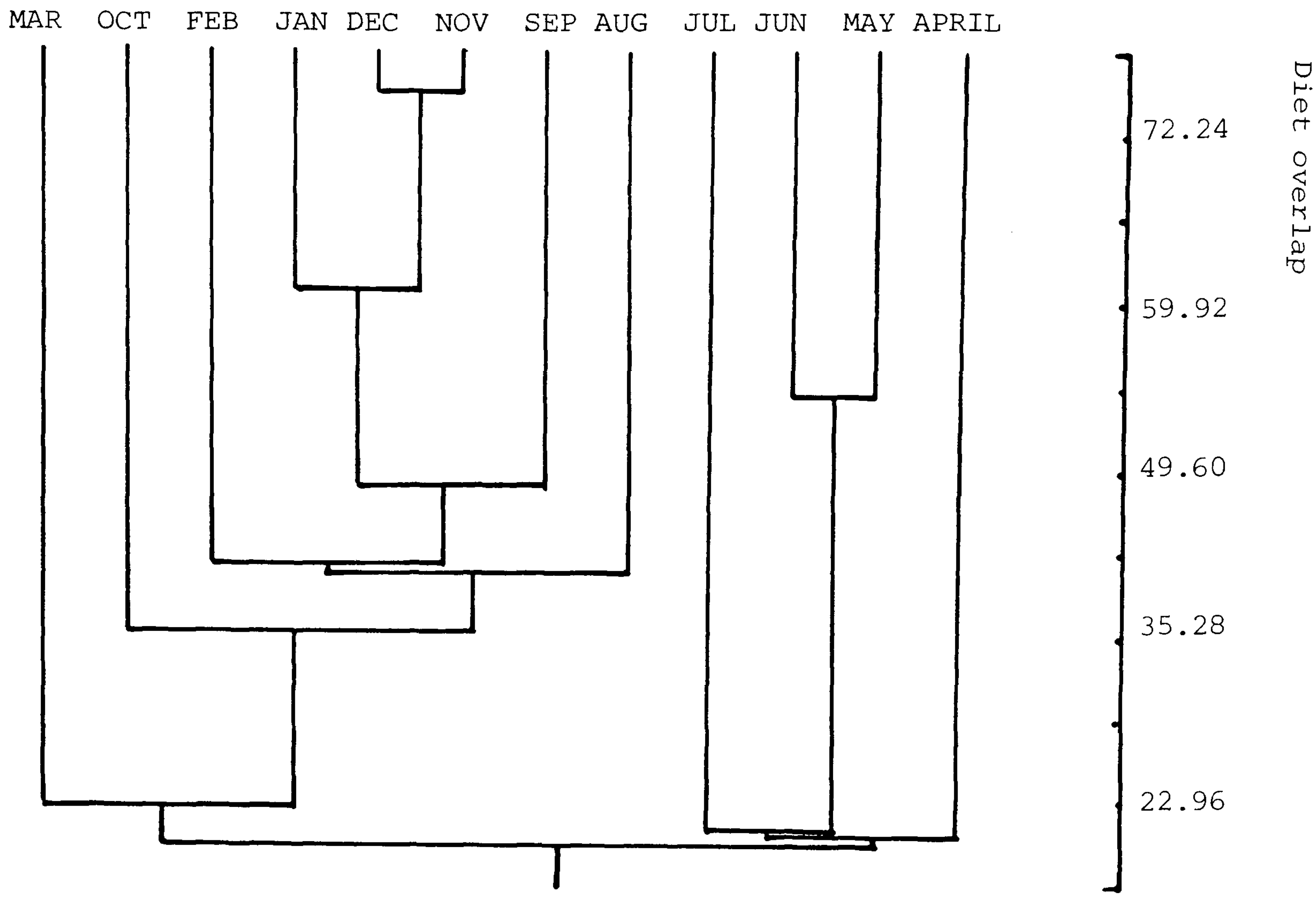


FIG 9.8 SINGLE LINKAGE DENDROGRAM OF % MONTHLY DIET OVERLAP.

Data in Appendix V. For item diets and species specfic diets.

a) Species specific items.



b) items.

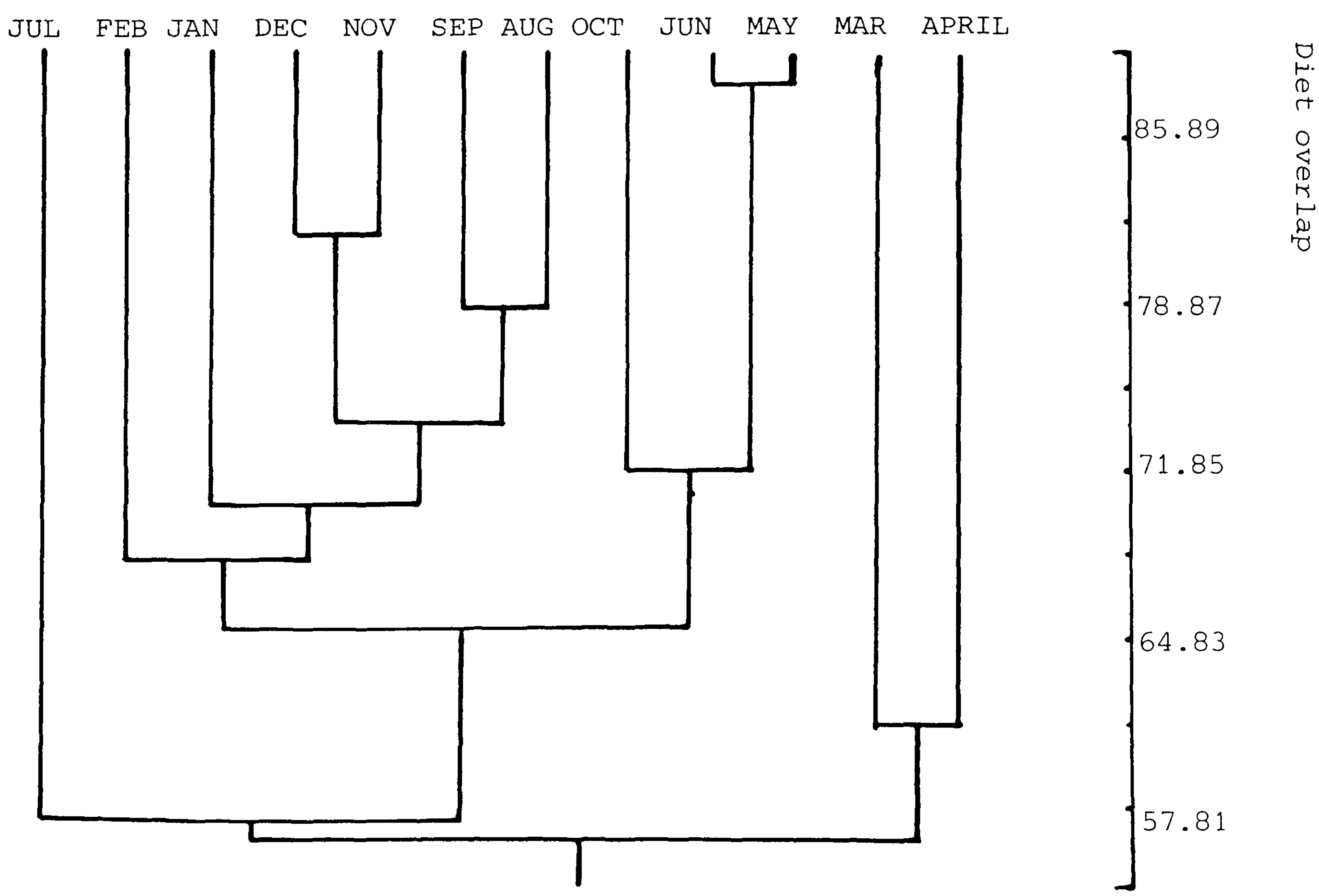


FIG 9.9 MONTHLY VARIATION IN % OF TIME SPENT FEEDING ON INVERTEBRATES, PETIOLES AND STEMS.

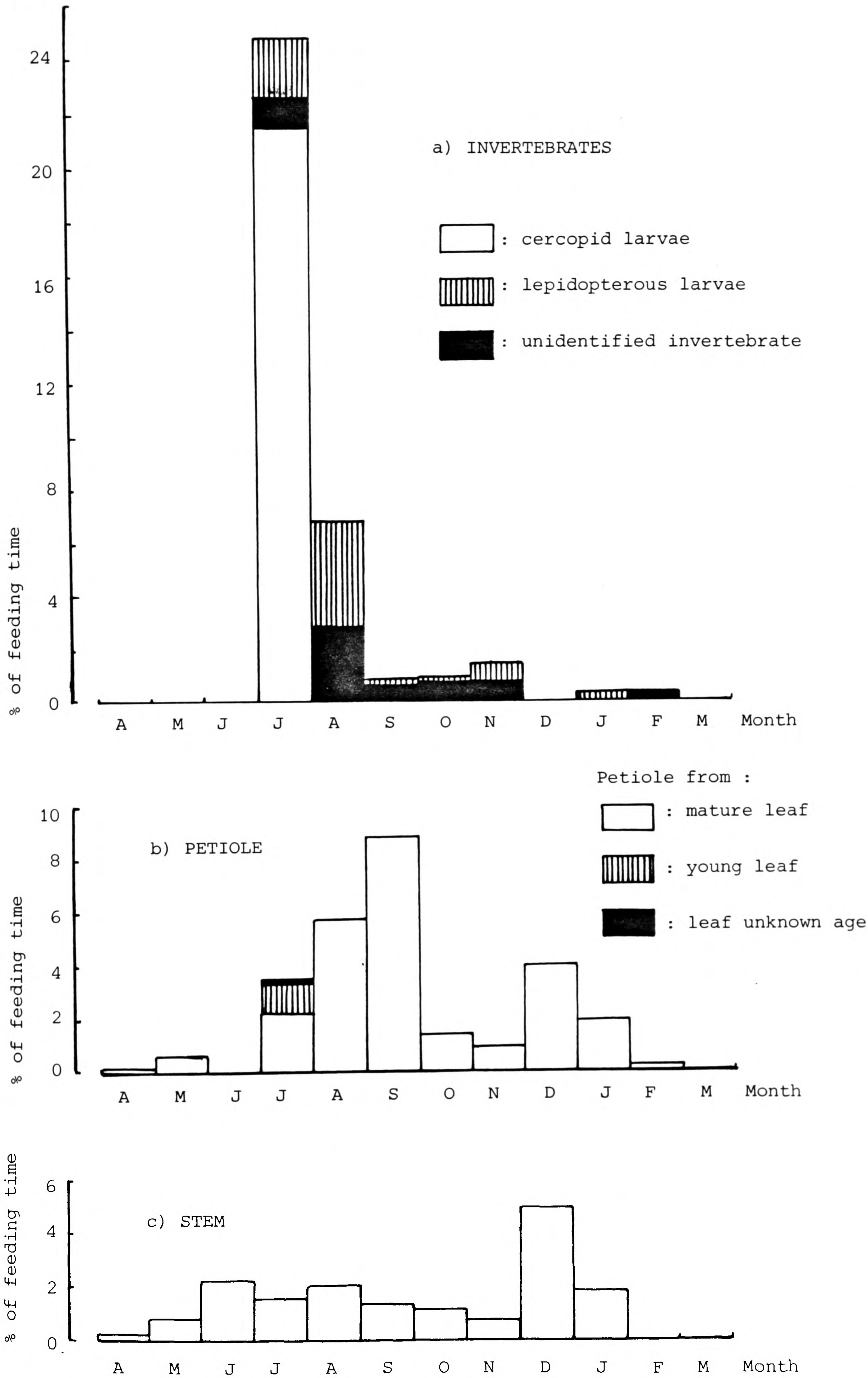
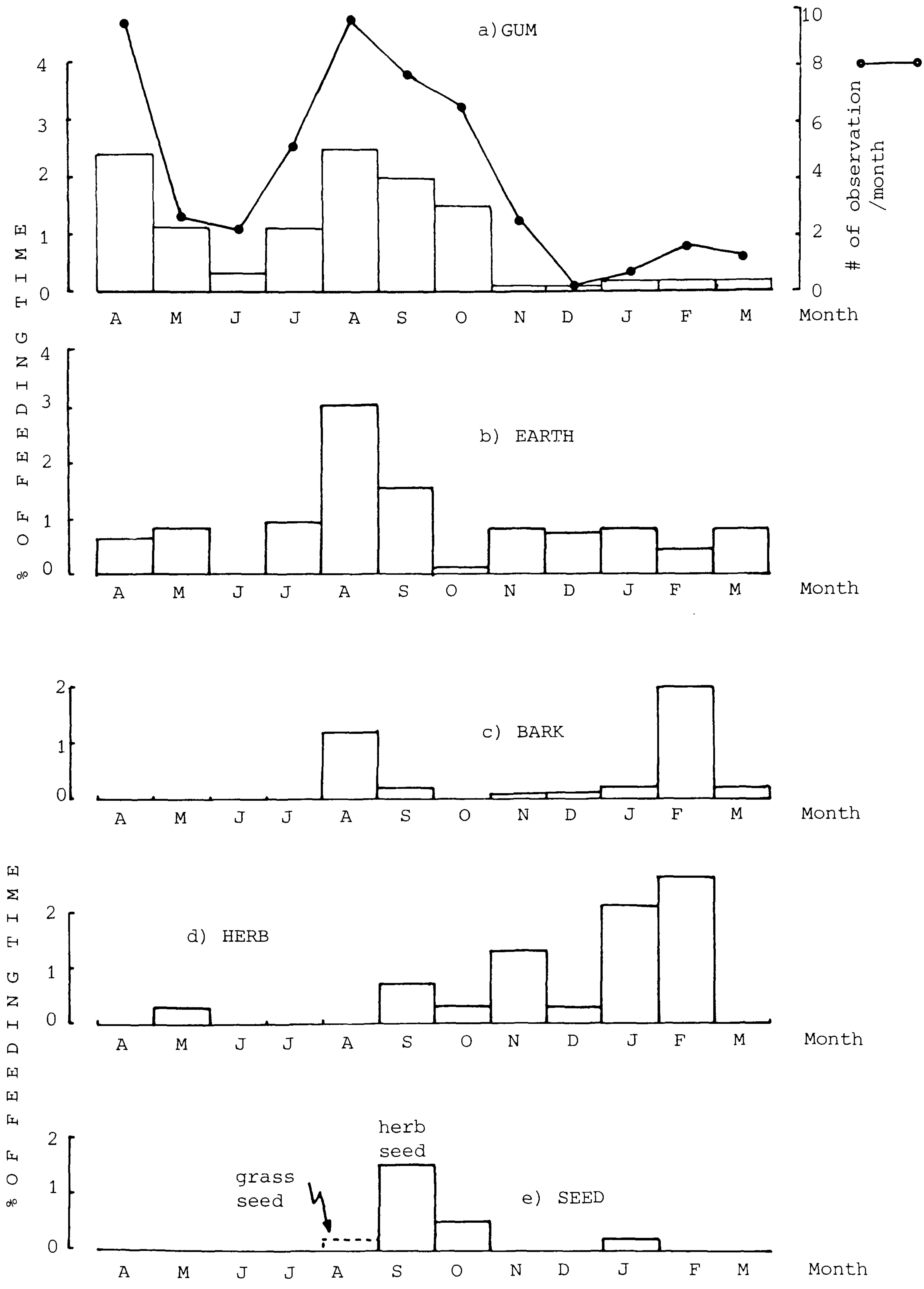


FIG 9.10 MONTHLY VARIATION IN % OF TIME SPENT FEEDING ON GUM, EARTH,BARK,HERB AND SEED.



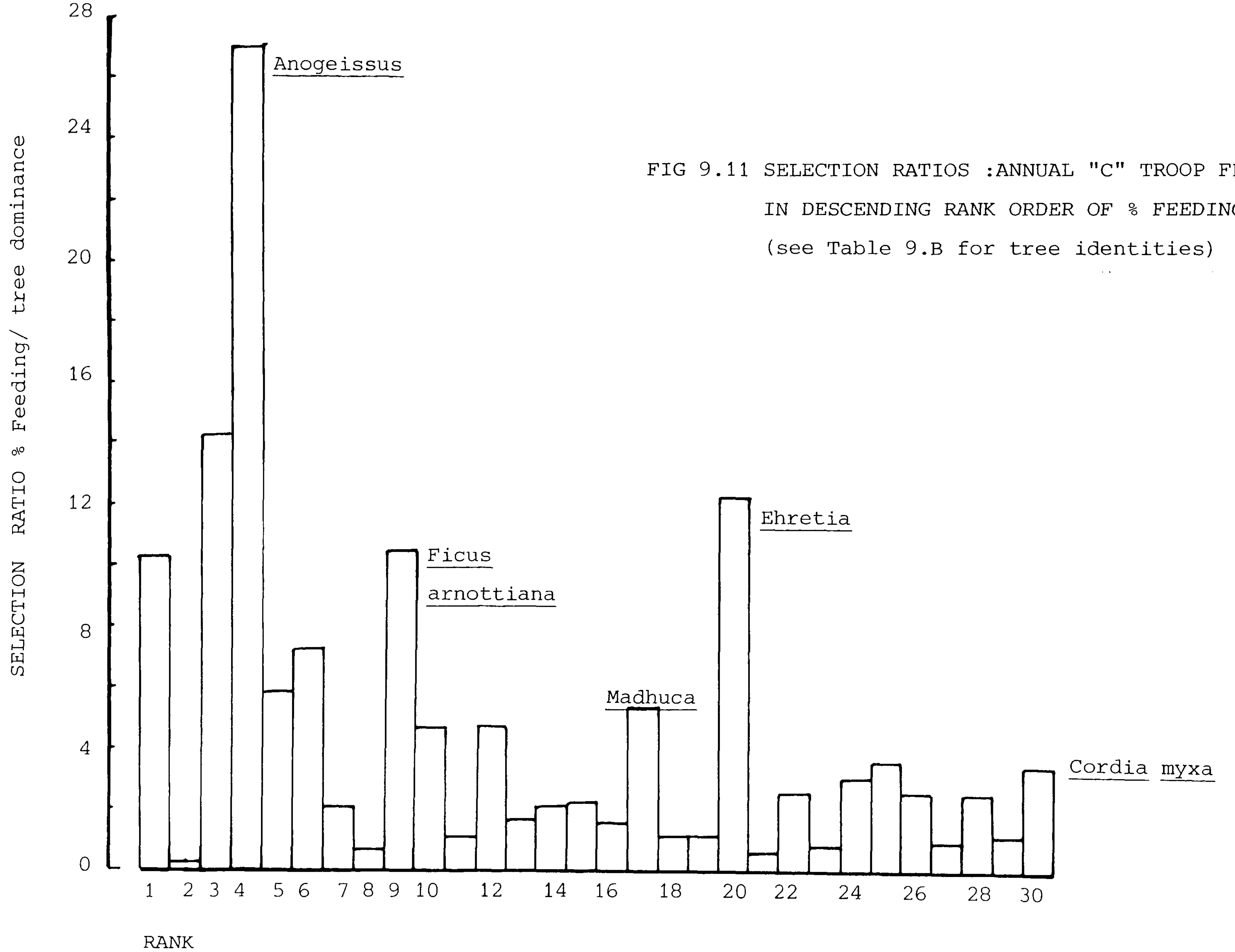


FIG 9.11 SELECTION RATIOS :ANNUAL "C" TROOP FEEDING BUDGET.
IN DESCENDING RANK ORDER OF % FEEDING TIME.
(see Table 9.B for tree identities)

FIG 9.12 RELATIONSHIP BETWEEN ITEM AVAILABILITY AND UTILIZATION FOR MATURE LEAF,YOUNG LEAF,LEAF BUD. Comparison of monthly item feeding budget and monthly availability index for April 1981-March 1982 (see text)

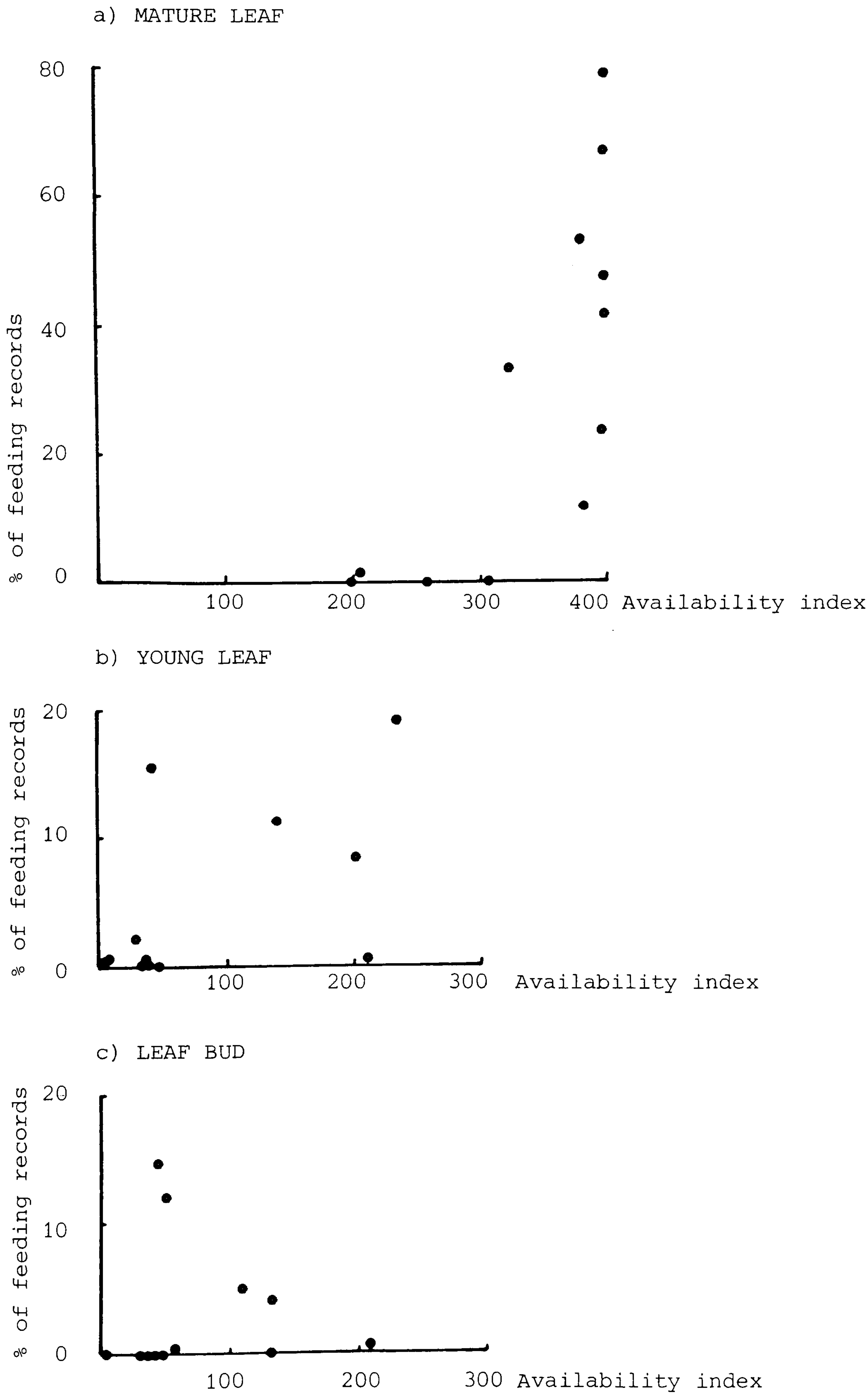


FIG 9.13 RELATIONSHIP BETWEEN ITEM AVAILABILITY AND UTILIZATION FOR FLOWERBUD,FLOWER AND FRUIT.

Comparison of monthly item feeding budget and monthly availability index for April 1981-March 1982 (see text)

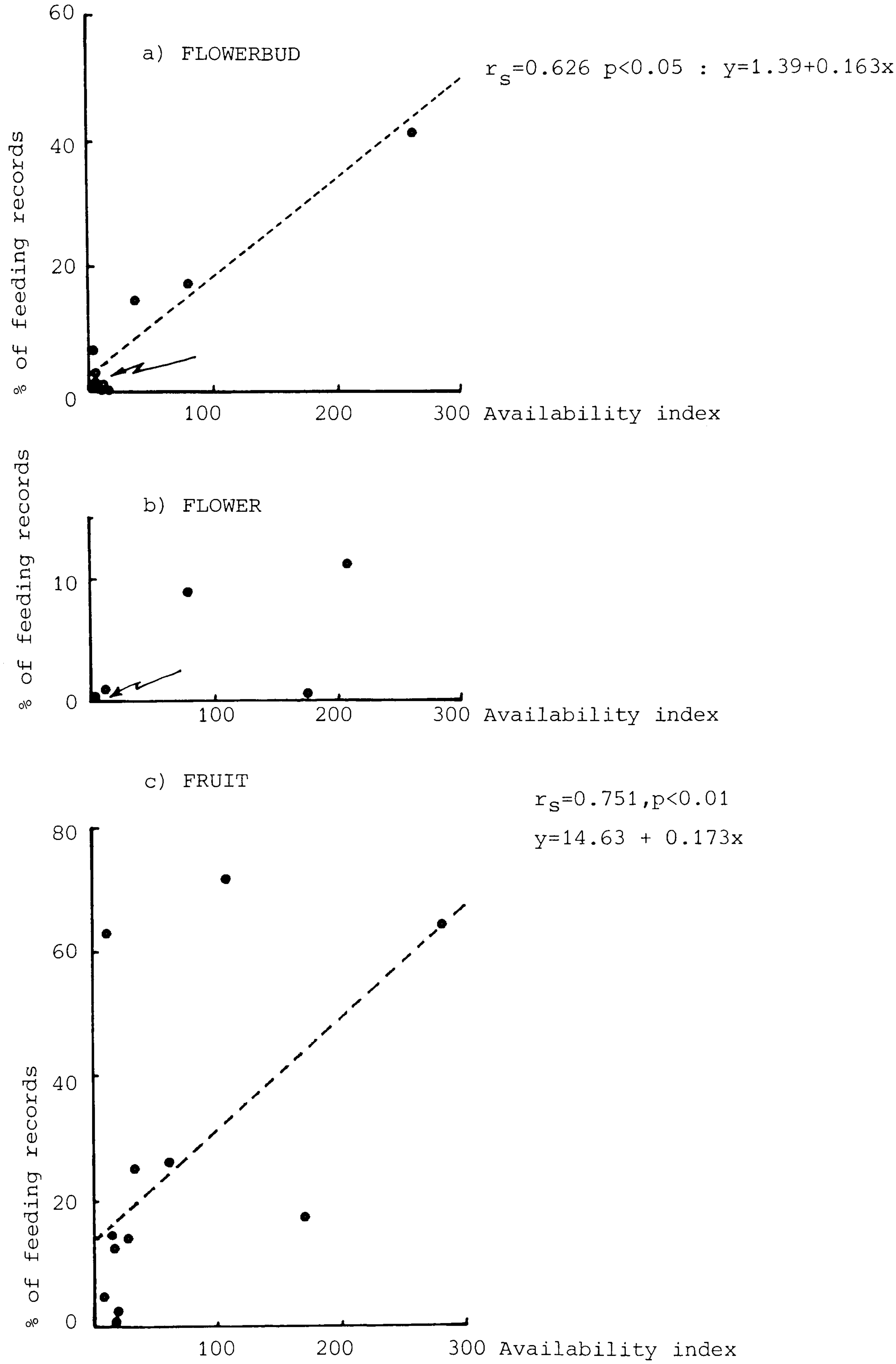


FIG 9.14 RELATIONSHIP BETWEEN ITEM AVAILABILITY AND UTILIZATION FOR OPEN LEAF BUD.

Comparison of monthly item feeding budget and monthly availability index for April 1981-March 1982 (see text)

r_s=0.830 $p<0.01$; $y=2.531 + 0.856x$

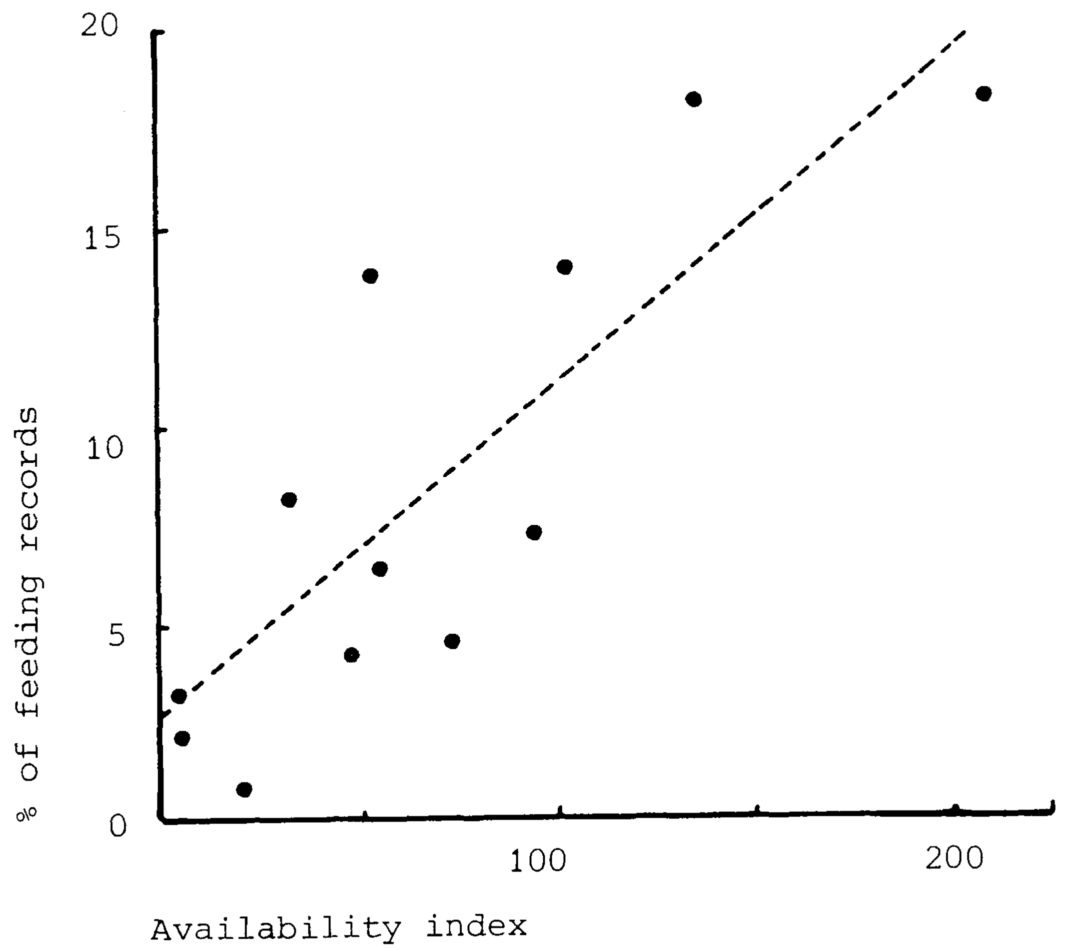


FIG 9.15 COMPARISON OF MONTHLY PATTERNS OF UTILIZATION AND AVAILABILITY FOR THREE TREE SPECIES SPECIFIC ITEMS.
(— — — — =utilization, ——— =availability)

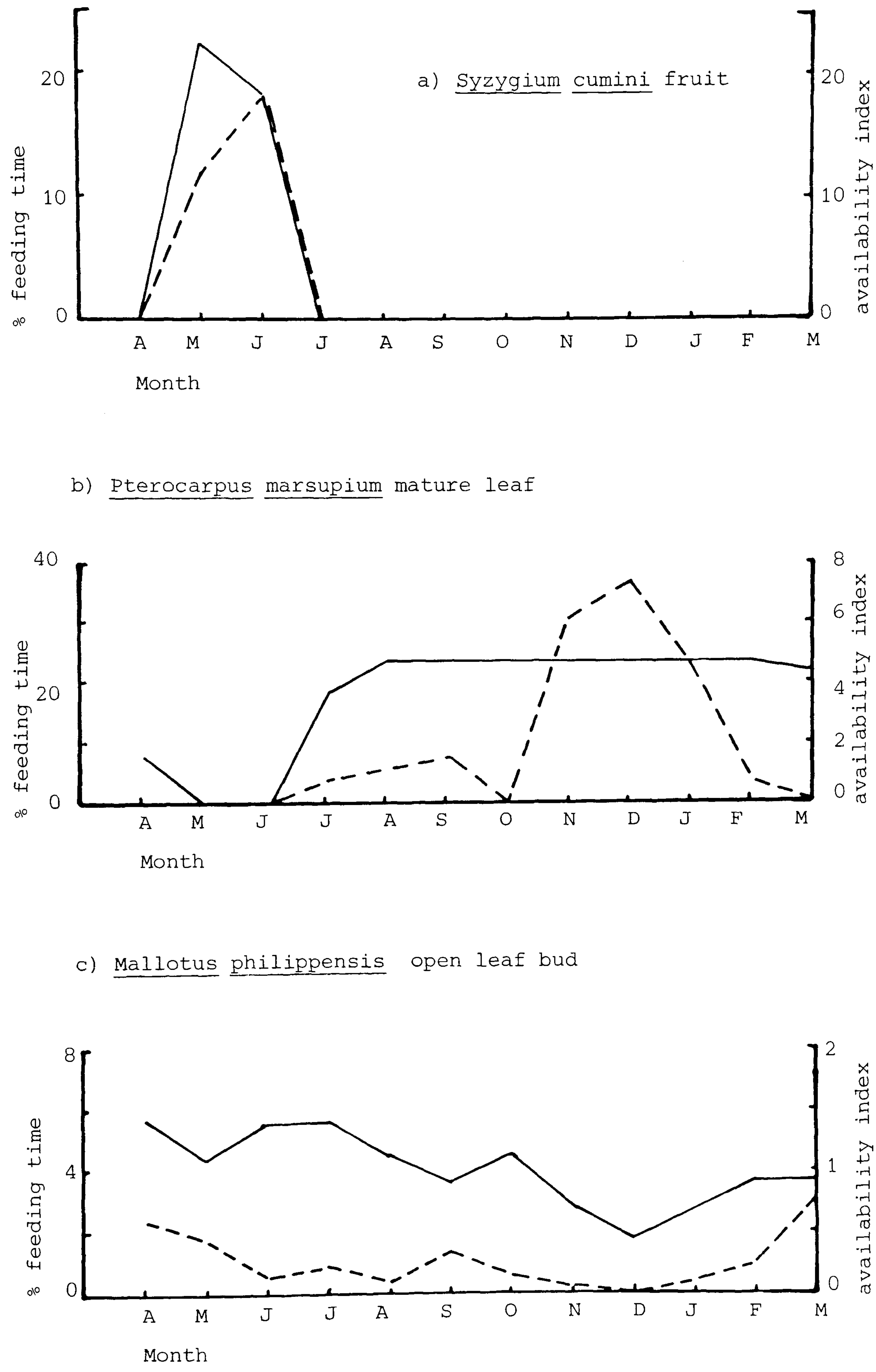
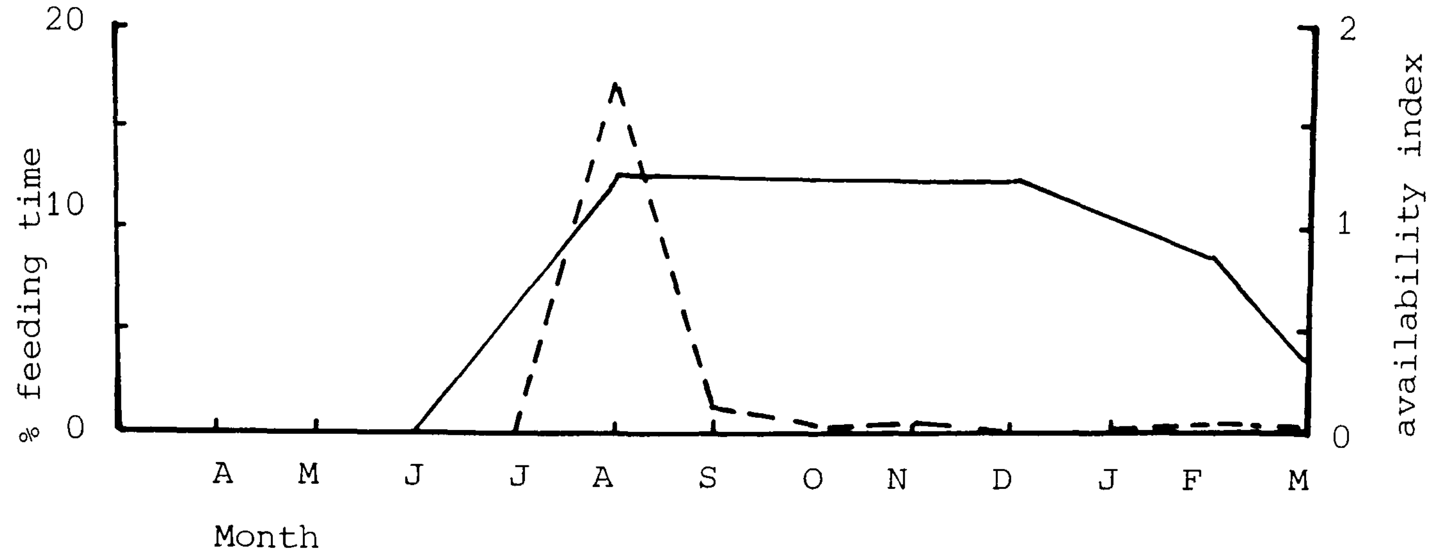


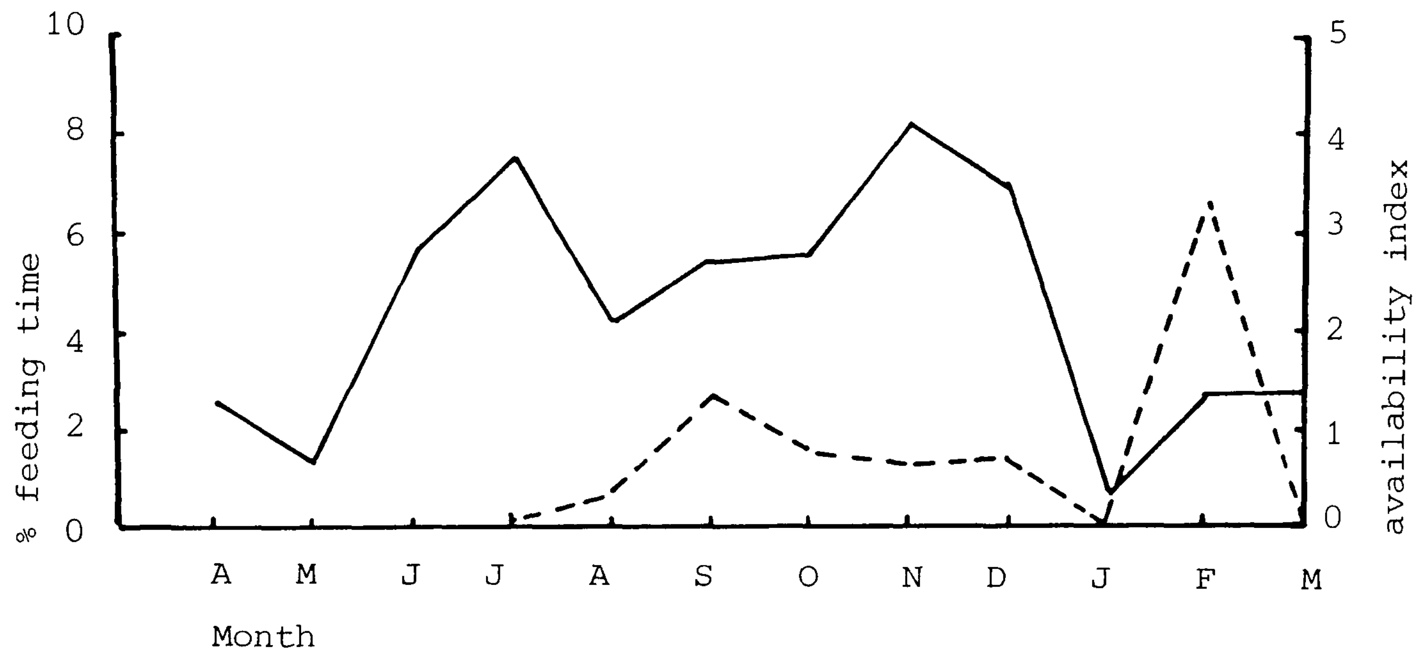
FIG 9.16 COMPARISON OF MONTHLY PATTERNS OF UTILIZATION AND AVAILABILITY FOR THREE TREE SPECIES SPECIFIC ITEMS.

(— — — — =utilization, ——— =availability)

a) Ficus arnottiana mature leaf



b) Ficus tomentosa fruit



c) Ficus infectoria fruit

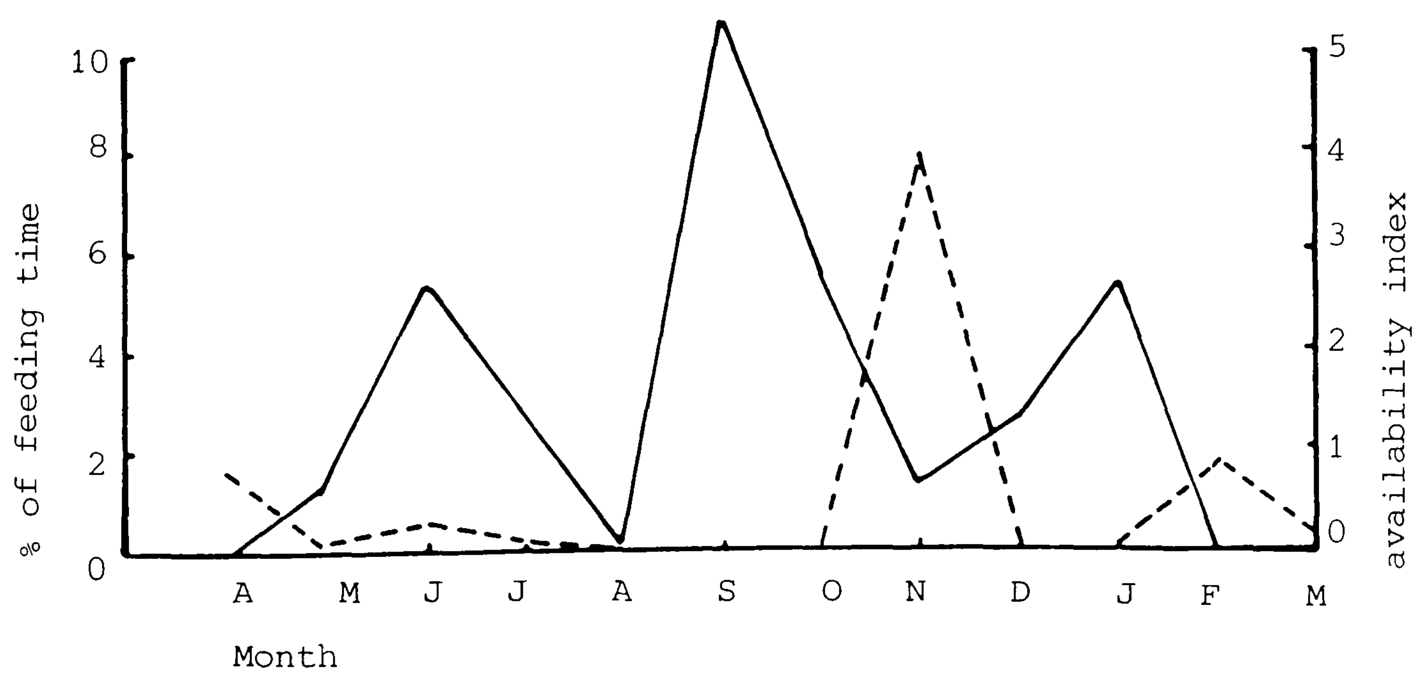


FIG 9.17 COMPARISON OF UTILIZATION AND AVAILABILITY OF TREE GUM FROM NINE SPECIES

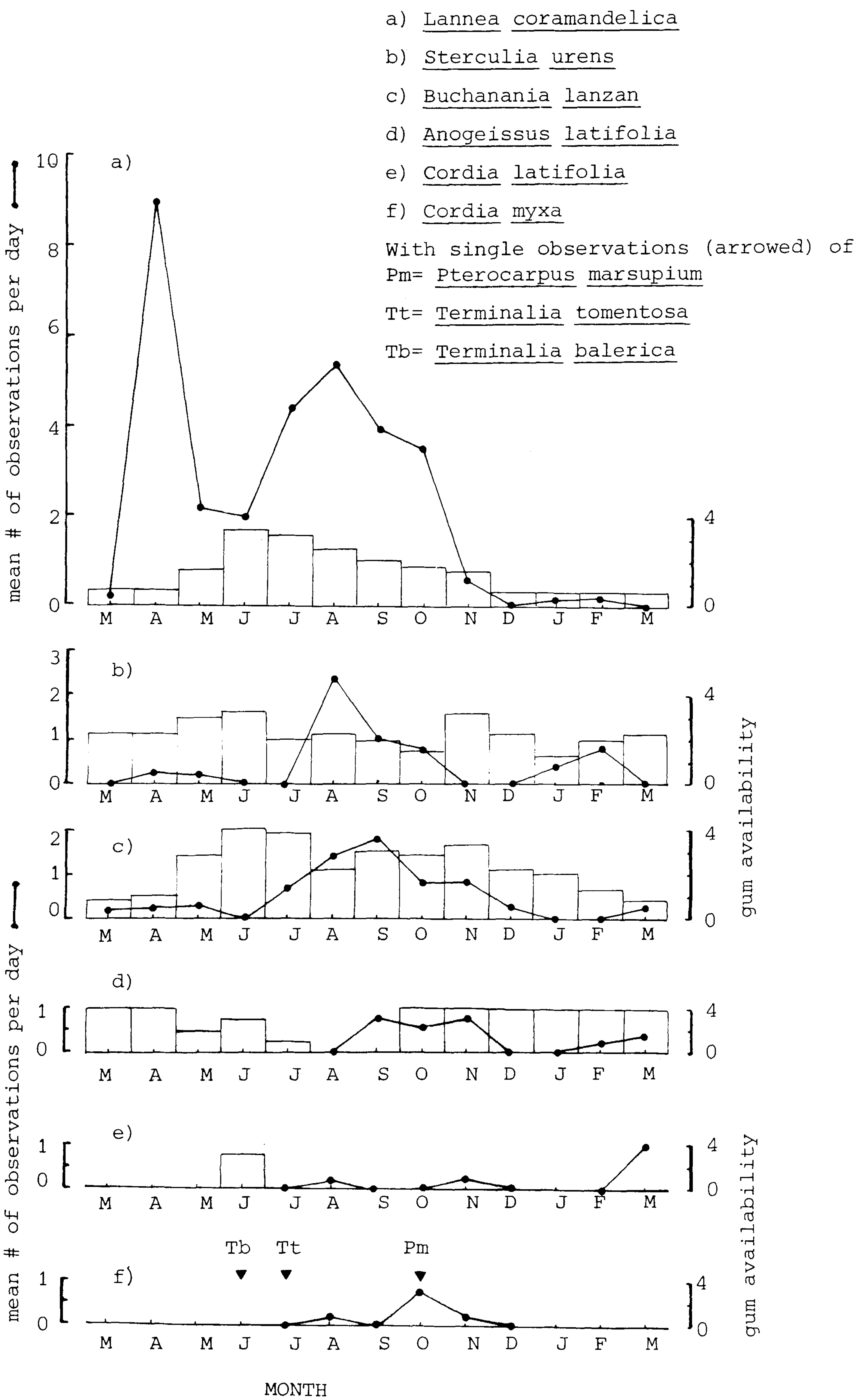


FIG 9.18 SKETCH OF A LANNEA CORAMANDELICA TREE SHOWING THE LOCATION AND TYPE OF GUM SITES AT WHICH LANGURS FEED.

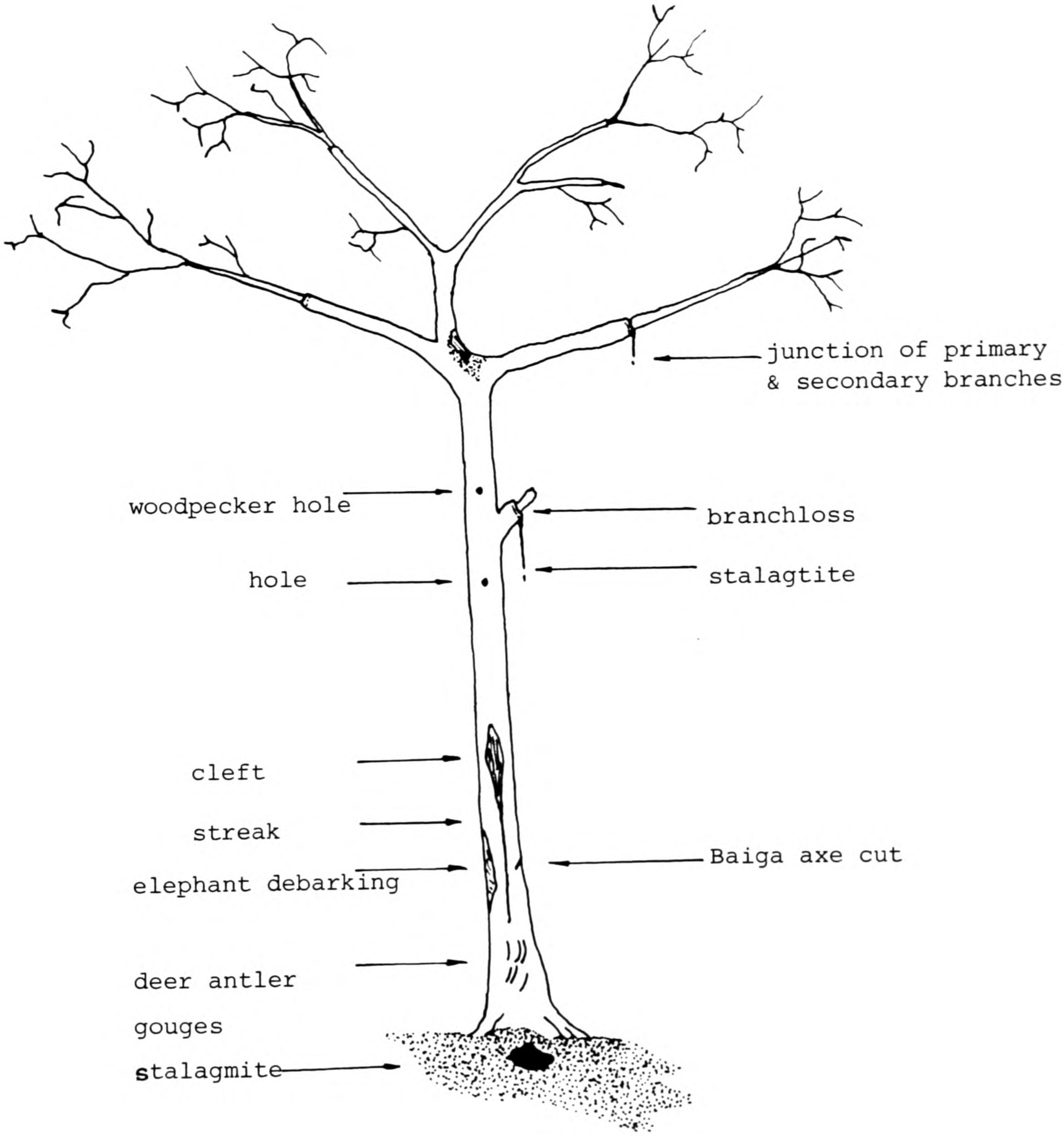


FIG 9.19 MONTHLY VARIATION IN DRINKING FREQUENCY "C" TROOP

Expressed as # of opportunistic observations > 1 langur seen to drink in 12 days per month.

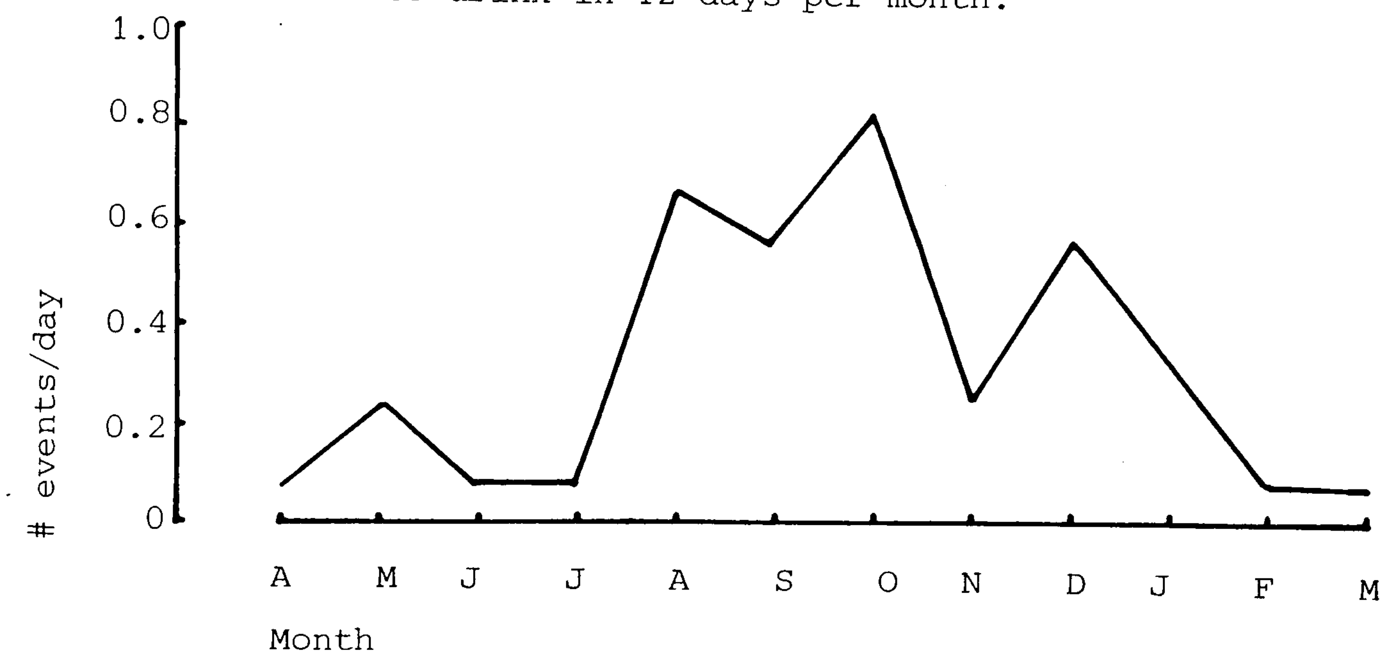


TABLE 9.A ANNUAL FEEDING BUDGET:BY ITEMS. N=6787.

Percentage of records

MONTH	N	Leaves ML	YL	LB	OB	LX	Petiole MP	YP	XP	Reproductive FB	FL	FR	Other ST	GU	BA	HE	HS	GS	Invert. EA	XI	Le	Ce	X
APRIL	491		8.8	14.9	14.1		0.2			15.3	21.4	17.7	0.2	2.4					0.6				4.5
MAY	355		19.4	0.6	4.5		0.6				0.3	64.8	0.8	1.1		0.3			0.8				6.8
JUNE	323		11.5	0.9	7.4							72.4	2.2	0.3									5.3
JULY	463	10.6	15.6		6.3	0.4	2.2	1.1	0.2		0.2	26.6	1.5	1.1					0.9	1.1	2.2	21.6	8.6
AUGUST	594	41.9	2.0		1.0	0.2	5.7					25.6	2.0	2.5	1.2			0.2	.0	2.9	4.0		8.6
SEPTEMBER	547	47.9	0.9		3.3	1.3	8.8			7.3		14.1	1.3	2.0	0.2	0.7	1.5		1.5	0.7	0.2		8.4
OCTOBER	887	23.0	0.3	0.1	2.3	0.1	1.4			2.7		63.7	1.1	1.5		0.3	0.5		0.1	0.8	0.2		1.8
NOVEMBER	757	67.9	0.3		8.2	0.1	0.9					13.7	0.7	0.1	0.1	1.3			0.8	0.8	0.7		4.4
DECEMBER	757	79.3			4.2		4.0					2.2	4.9	0.1	0.1	0.3			0.7				4.2
JANUARY	513	53.2	0.2	12.5	13.8		1.9			0.8		0.2	1.8	0.2	0.2	2.1	0.2		0.8		0.4		11.7
FEBRUARY	502	33.5	0.6	4.6	18.3		0.2			16.9		8.8		0.2	2.0	2.6			0.4	0.4			11.6
MARCH	504	1.4	0.2	5.2	18.3					42.7	17.5	2.6		0.2	0.2				0.8				11.1
ANNUAL * BUDGET	6787	34.9	3.6	2.8	7.9	0.1	2.4	–	–	6.6	2.9	24.5	1.5	1.0	0.3	0.7	0.2	–	0.9	0.6	0.7	1.5	6.8

(*September representation in annual budget weighted by 7/6 to compensate for smaller sample size.)

Abbreviations :

N = Number of records
ML = Mature leaf
YL = Young leaf
LB = Leaf bud (unopen)
OB = Open leaf bud
LX = Leaf of unknown age
MP = Mature leaf petiole
YP = Young leaf petiole
XP = Petiole of unknown age
FB = Flower bud (unopen)
FL = Flower
FR = Fruit
ST = Stem
GU = Gum
BA = Bark
HE = Herb
HS = Herb seed
GS = Grass seed
EA = Earth
XI = Invertebrate of unknown taxa
Le = Lepidopterous larvae
Ce = Cercopid
X = Item unknown
Invert = Invertebrate

TABLE 9.B ANNUAL FEEDING BUDGET:BY ITEM AND SPECIES. N= 6787

For abbreviations see Table 9.A

Species	Rank	Total	Percentage of feeding records: Leaves					Petiole			Reproductive			Other				Invertebrate			
			ML	YL	LB	OB	LX	MP	YP	XP	FB	FL	FR	ST	GU	BA	EA	XI	Le	Ce	X
Pterocarpus m.	1	12.23	11.20	0.13		0.24	0.01	0.01			0.24				0.01						0.30
Shorea r.	2	12.08		0.01	0.16	3.05		0.01			2.48	0.46	3.85	0.01				0.25	0.13		1.67
Flamengia s.	3	9.17		0.18		0.03							8.93								0.03
Bauhinia r.	4	7.01	5.86	0.43				0.01			0.18			0.06				0.09	0.22		0.16
Anogeissus l.	5	5.94	4.76		0.56	0.24					0.04		0.01	0.01	0.03						0.28
Saccopetalum t.	6	5.01	2.55					0.01			0.31	0.13	1.86	0.01							0.11
Emblica o.	7	4.21	1.49	0.24	0.01	0.07							1.96							0.06	0.38
Terminalia c.	8	3.48	1.12	0.04		0.04		1.68	0.01	0.01	0.04		0.40			0.01					0.10
Syzygium c.	9	3.46		0.03	0.22	1.16							1.52					0.06	0.03		0.44
Ficus a.	10	3.18	1.83	0.13		0.04						0.01	0.19						0.06	0.74	0.18
Lannea c.	11	3.05	1.86	0.01	0.01								0.19		0.59			0.04	0.03	0.25	0.06
Ficus i.	12	2.87		0.03	0.99	0.35							1.22	0.01		0.10					0.16
Terminalia t.	13	2.76	2.09	0.03				0.34	0.03										0.01	0.11	0.10
Ficus t.	14	2.27	0.01	0.28		0.16							1.42	0.01						0.16	0.22
Terminalia b.	15	1.90	0.10	0.09	0.46	0.35		0.03	0.01		0.06		0.27	0.31							0.22
Mallotus p.	15	1.90	0.01	0.16	0.01	0.91	0.01				0.60	0.01	0.03								0.13
Bauhinia v.	16	1.65		0.01							0.15	1.14	0.28	0.01							0.06
Cordia l.	17	1.42	0.69	0.03								0.03	0.63				0.03				
Madhuca i.	18	1.24									0.65		0.09	0.47							0.03
Ougenia d.	19	1.22				0.01					0.18	0.83						0.04	0.03		0.13
Stereosperm s.	20	1.14		0.32		0.04					0.43	0.16	0.13							0.01	0.03
Ehretia l.	21	1.09		0.16		0.25					0.57	0.03									0.07
Holarrhena a.	22	0.85	0.46	0.01	0.01	0.01	0.01	0.06								0.21		0.03	0.01		0.03
Butea m.	23	0.78	0.01	0.35		0.01					0.29			0.04							0.06
Sterculia u.	24	0.72						0.03	0.01			0.03	0.28	0.10	0.27						
Bombax c.	25	0.65		0.11		0.03		0.21			0.24		0.06								
Bauhinia l.	26	0.63	0.06	0.31		0.15	0.06				0.04										0.01
Zizyphus x.	27	0.62	0.25	0.01			0.03						0.29	0.01							0.01
Albizzia o.	28	0.53		0.03	0.24	0.21						0.01	0.04								
Litsea s.	29	0.34	0.10	0.09	0.01	0.12															0.01
Dendrocalmus s	30	0.32		0.01										0.31							
Bauhinia m.	31	0.28	0.01	0.10									0.15								0.01

TABLE 9.B (CONTD.).

Species	Rank	Total	Percentage of feeding records: Leaves					Petiole			Reproductive			Other				Invertebrate			
			ML	YL	LB	OB	LX	MP	YP	XP	FB	FL	FR	ST	GU	BA	EA	XI	Le	Ce	X
Schleichera o.	31	0.28	0.01			0.07					0.06	0.03	0.03					0.4	0.01		0.01
Cordia m.	32	0.27	0.19										0.06								0.01
Bridelia r.	33	0.25		0.09		0.10							0.04								0.01
Careya a.	34	0.19			0.12	0.01							0.03								0.03
Zizyphus r.	35	0.18		0.01	0.01	0.03							0.12								
Lagerstroemia	36	0.15																	0.01	0.70	0.03
Litsea p.	36	0.15	0.09	0.04		0.01															
Diospyros m.	37	0.13						0.03					0.07								0.03
Ficus p.	38	0.10				0.01							0.06								0.03
Semecarpus a.	38	0.10																0.04	0.04	0.01	
Ficus c.	38	0.10											0.10								
Buchanania l.	38	0.10											0.03		0.07						
Specimen #205	39	0.06	0.01	0.03		0.01															
Ficus r.	39	0.06				0.03							0.01								0.01
Pheonix a.	40	0.04									0.04										
Ipomea spp.	40	0.04	0.03			0.01															
Woodfordia f.	40	0.04	0.03			0.01															
Stereosperm x.	41	0.03									0.03										
Cassia f.	41	0.03																	0.01		0.01
Placourtia	42	0.01		0.01																	
Grewia t.	42	0.01																		0.01	
Glochidion v.	42	0.01																0.01			
Embelia r.	42	0.01											0.01								
Flamengia m.	42	0.01											0.01								
Casearia g.	42	0.01	0.01																		
Ficus g.	42	0.01				0.01															
Unknown spp.		0.03		0.03																	
Ground *		3.55	0.04	0.06		0.03	0.01						0.06	0.03	0.01				0.01		1.5
TOTAL			34.90	3.67	2.83	7.87	0.18	2.40	0.07	0.01	6.63	2.8	24.46	1.46	0.99	0.32	0.87	0.62	0.66	1.47	6.82

(*plus herb 0.66%, earth 0.84%, herb seed 0.21%, grass seed 0.01%.)

TABLE 9.C MONTHLY FEEDING BUDGETS.
For abbreviations see Table 9.A.

APRIL 1981: N=491

Percentage of feeding records.

Species	Rank	Total	Leaves					Petiole			Reproductive			Other							Invert.			
			ML	YL	LB	OB	LX	MP	YP	XP	FB	FL	FR	ST	GU	BA	HE	HS	GS	EA	XI	Le	Ce	X
Bauhinia v.	1	17.9									2.0	15.7												0.2
Terminalia b.	2	11.8			6.3	4.3					0.8													0.4
Anogeissus l.	3	9.6			7.7	1.6					0.2													
Shorea r.	4	8.8										0.2	8.4											0.2
Stereopermum s.	5	8.1									5.9	2.2												
Saccopetalum t.	6	5.9									4.3	1.6												
Sterculia u.	7	4.3										0.4	3.9											
Bauhinia r.	8	4.1		3.3		0.2					0.6													
Ehretia l.	9	3.3		2.0		1.2																		
Albizzia o.	10	3.1		0.4	0.6	1.8						0.2												
Bombax c.	11	2.6		1.4		0.4							0.8											
Mallotus p.	12	2.4				2.4																		
Lannea c.	12	2.4			0.2										2.2									
Ficus i.	13	2.0				0.4							1.6											
Cordia l.	14	1.8										0.4	1.4											
Other species (11)		7.0		1.6		1.6		0.2			1.4	0.6	1.2											0.2
Other ground		4.7											0.4		0.2					0.6				3.5
TOTAL				8.8	14.9	14.1		0.2			15.3	21.4	17.7		2.4					0.6				4.5

TABLE 9.C (Contd.) MONTHLY FEEDING BUDGETS.

MAY 1981 : N=355

Species	Rank	Total	Percentage of feeding records																				
			Leaves					Petiole			Reproductive			Other							Invert.		
			ML	YL	LB	OB	LX	MP	YP	XP	FB	FL	FR	ST	GU	BA	HE	HS	GS	EA	XI	Le	Ce	X
Shorea r.	1	22.5											21.7	0.3										0.6
Syzygium c.	2	12.4											12.4											
Saccopetalum t.	2	12.4										0.3	11.0											1.1
Cordia l.	3	9.9											9.6							0.3				
Stereospermum s.	4	8.5		5.9									2.5											
Butea m.	5	4.5		4.5																				
Lannea c.	6	4.2											3.7		0.6									
Flamengia s.	7	3.7		3.1		0.3							0.3											
Mallotus p.	8	2.8		0.6	0.3	1.7							0.3											
Terminalia b.	9	2.5		1.1		0.6		0.3																0.6
Bauhinia m.	10	2.0		2.0																				
Bridelia r.	11	1.4		1.4																				
Zizyphus r.	11	1.4											1.4											
Pterocarpus m.	12	1.1				1.1																		
Buchanania l.	13	0.8											0.6		0.3									
Other species (14)		5.9		0.6	0.3	0.9		0.3					1.2	0.6	0.3									1.8
Other ground				0.3									0.3				0.3			0.6				2.8
TOTAL				19.4	0.6	4.5		0.6				0.3	64.8	0.8	1.1		0.3			0.8				6.8

TABLE 9.C (Contd.) MONTHLY FEEDING BUDGETS.

JUNE 1981: N=323

Species	Rank	Total	Percentage of feeding records: Leaves ML	YL	LB	OB	LX	Petiole MP	YP	XP	Reproductive FB	FL	FR	Other ST	GU	BA	HE	HS	GS	EA	Invert. XI	Le	Ce	X
Shorea r.	1	29.7											29.7											
Saccopetalum t.	2	21.1											21.1											
Syzygium c.	3	18.3											18.3											
Bauhinia r.	4	8.0		8.0																				
Pterocarpus m.	5	4.6		0.3		2.8																		1.5
Bridelia retusa	6	2.8		0.3		2.2																		0.3
Dendrocalmus s.	7	2.2		0.3										1.9										
Madhuca indica	8	1.9											1.5											0.3
Zizyphus r.	9	1.2		0.3	0.3	0.6																		
Stereospermum s.	9	1.2		0.3		0.9																		
Terminalia b.	10	0.9		0.6									0.3											
Butea m.	10	0.9		0.6										0.3										
Ficus i.	11	0.6											0.6											
Cordia l.	11	0.6											0.6											
Mallotus p.	11	0.6				0.6																		
Other tree spp.(8)		3.6		0.6	0.6	0.3							0.3		0.3									0.9
Other ground																								2.2
TOTAL				11.5	0.9	7.4							72.4	2.2	0.3									5.3

TABLE 9.C (Contd.) **MONTHLY FEEDING BUDGETS.**

JULY 1981: N=463

Percentage of feeding records

Species	Rank	Total	Leaves				Petiole				Reproductive			Other							Invert.			
			ML	YL	LB	OB	LX	MP	YP	XP	FB	FL	FR	ST	GU	BA	HE	HS	GS	EA	XI	Le	Ce	X
Ficus a.	1	13.2		1.9		0.4							1.3										10.8	
Ficus t.	2	12.7		4.1		2.4																	2.4	2.6
Shorea r.	3	9.7											9.1								0.2			0.4
Terminalia t.	4	7.1	2.8					1.7	0.4														1.7	0.4
Pterocarpus m.	5	6.7	3.9	1.7		0.6	0.2																	0.2
Lannea c.	6	5.8	0.9	0.2											1.1								3.7	
Terminalia b.	7	5.6	0.2			0.2		0.2	0.2				2.2	0.6										1.9
Terminalia c.	8	5.4		0.6		0.2		0.2	0.2	0.2			3.7											0.2
Saccopetalum t.	9	4.3											4.3											
Bauhinia v.	10	3.9											3.9											
Mallotus p.	11	3.5		1.7		0.9						0.2												0.6
Bauhinia r.	12	3.2		0.6																	0.4	2.2		
Emblica o.	13	2.8		1.1		0.2																	0.9	0.6
Cordia m.	14	2.6	1.9										0.6											
Litsea s.	15	2.2		1.3		0.6																		0.2
Other tree spp.(20)			0.8	1.4		0.6	0.2		0.2				1.4	0.8						0.9	0.4		2.1	0.8
Other ground				0.6																				
TOTAL			10.6	15.3		6.3	0.4	2.2	1.1	0.2		0.2	26.6	1.5	1.1					0.9	1.1	2.2	21.6	8.6

TABLE 9.C (Contd.) MONTHLY FEEDING BUDGETS.

AUGUST 1981: N=594

Species	Rank	Total	Percentage of feeding records: Leaves ML	YL	LB	OB	LX	Petiole MP	YP	XP	Reproductive FB	FL	FR	Other ST	GU	BA	HE	HS	GS	EA	Invert. XI	Le	Ce	X
Emblica o.	1	23.6		1.7									19.2											2.7
Ficus a.	2	18.4	17.2										0.3											0.8
Pterocarpus m.	3	7.8	6.7																					1.0
Terminalia c.	4	6.9	0.5					4.6					1.3											0.5
Saccopetalum t.	5	6.7	6.2					0.2																0.3
Lannea c.	6	6.6	4.6												0.8						0.5	0.3		0.3
Zizyphus x.	7	3.7	0.7										2.9											0.2
Shorea r.	8	3.0											0.8								1.0	1.2		
Bauhinia r.	8	3.0	1.9																		0.5	0.7		
Sterculia u.	8	3.0						0.3						1.0	1.7									
Terminalia t.	9	2.2	0.8					0.7														0.2		0.5
Cordia l.	10	1.3	1.3																					
Ficus i.	11	1.2														1.2								
Dendrocalmus s.	12	1.0												1.0										
Anogeissus l.	12	1.0				0.5																		0.5
Other tree spp(14)		6.1	1.2	0.4		0.5	0.2						0.9								0.9	1.5		1.2
Other ground													0.2						0.2	3.0		0.2		0.7
TOTAL			41.9	2.0		1.0	0.2	5.7					25.6	2.0	2.5	1.2			0.2	3.0	2.9	4.0		8.6

TABLE 9.C (Contd.) MONTHLY FEEDING BUDGETS.

SEPTEMBER 1981: N=547

Species	Rank	Total	Percentage of feeding records																				
				Leaves				Petiole			Reproductive			Other							Invert.		
			ML	YL	LB	OB	LX	MP	YP	XP	FB	FL	FR	ST	GU	BA	HE	HS	GS	EA	XI	Le	Ce	X
Anogeissus l.	1	14.1	11.7								0.4				0.2									1.8
Pterocarpus m.	2	11.5	7.5								2.2													1.8
Terminalia c.	3	10.6	2.6					7.5					0.2			0.2								0.2
Bauhinia r.	4	9.7	6.2								1.8											0.2		1.5
Emblica o.	5	6.6	2.9										2.9											0.7
Saccopetalum t.	6	5.5	5.3																					0.2
Lannea c.	7	5.3	4.2												1.1									
Mallotus p.	8	4.9				1.3	0.2				2.9													0.6
Flamengia s.	9	4.6											4.6											
Terminalia t.	10	3.1	2.2					0.9																
Bauhinia m.	10	3.1	0.6	0.7		1.1	0.6																	0.2
Ficus a.	11	2.7	1.5										1.3											
Ficus t.	11	2.7											2.7											
Cordia l.	12	2.4	2.4																					
Terminalia b.	13	2.2	0.6										1.1	0.4										0.2
Other tree spp	(15)	6.8	0.4	0.2		0.9	0.6	0.4					1.3	0.9	0.8						0.7			0.6
Other ground		4.4															0.7	1.5		1.5				0.7
TOTAL			47.9	0.9		3.3	1.3	8.8			7.3		14.1	1.3	2.0	0.2	0.7	1.5		1.5	0.7	0.2		8.4

TABLE 9.C (Contd.) MONTHLY FEEDING BUDGETS.

OCTOBER 1981: N=887

Species	Rank	Total	Percentage of feeding records: Leaves ML	YL	LB	OB	LX	Petiole MP	YP	XP	Reproductive FB	FL	FR	Other ST	GU	BA	HE	HS	GS	EA	Invert. XI	Le	Ce	X
Flamengia s.	1	61.9											61.9											
Anogeissus l.	2	4.3	4.1			0.2																		
Lannea c.	2	4.3	3.4												0.9									
Terminalia c.	3	3.7	2.6					0.9																0.2
Emblica o.	4	3.5	3.5																					
Terminalia t.	5	3.4	3.4																					
Bauhinia r.	6	3.2	3.0																					0.1
Mallotus p.	7	3.0				0.6					2.5													
Shorea r.	8	2.3			0.1	1.5															0.2	0.1		0.3
Ficus t.	9	1.6											1.6											
Cordia l.	10	1.4	1.0	0.2																0.1				
Pterocarpus m.	11	1.2	0.8								0.2				0.1									0.1
Terminalia b.	12	1.0	0.1											0.9										
Ficus a.	13	0.9	0.9																					
Semecarpus a.	14	0.6																			0.3	0.2		
Other tree spp(13)		2.2	0.2	0.1			0.1	0.5					0.2	0.2	0.4						0.2			0.3
Other ground		1.5															0.3	0.5						0.7
TOTAL			23.0	0.3	0.1	2.3	0.1	1.4			2.7		63.7	1.1	1.5		0.3	0.5		0.1	0.8	0.3		1.8

TABLE 9.C (Contd.) MONTHLY FEEDING BUDGETS.

NOVEMBER 1981: N=757

Species	Rank	Total	Percentage of records: Leaves ML	YL	LB	OB	LX	Petiole MP	YP	XP	Reproductive FB	FL	FR	Other ST	GU	BA	HE	HS	GS	EA	Invert. XI	Le	Ce	X
Pterocarpus m.	1	31.0	30.8					0.1																0.1
Anogeissus l.	2	12.0	11.4										0.1		0.1									0.4
Bauhinia r.	2	12.0	11.8																		0.1			0.1
Shorea r.	3	10.8		0.1		8.1		0.1													0.4	0.1		2.0
Ficus i.	4	8.3											8.1											0.3
Terminalia t.	5	3.7	3.6	0.1																				
Flamengia s.	6	3.4											3.4											
Terminalia c.	7	2.8	2.2					0.5																
Lannea c.	8	2.5	2.4																					0.1
Emblica o.	9	2.1	2.1																					
Holarrhena a.	10	1.7	1.4					0.1								0.1								
Ficus a.	11	1.6	0.1										0.1									0.5		0.8
Saccopetalum t.	11	1.6	1.6																					
Ficus t.	12	1.3											1.3											
Bridelia r.	13	0.4											0.4											
Other tree spp (9)		1.9	0.5			0.1							0.7								0.3			0.1
Other ground		9.6					0.1							0.7			1.3			0.8				0.4
TOTAL			67.9	0.3		8.2	0.1	0.9					13.7	0.7		0.1	1.3			0.8	0.8	0.7		4.4

TABLE 9.C (Contd.) **MONTHLY FEEDING BUDGETS.**

DECEMBER 1981: N=757

Species	Rank	Total	Percentage of records: Leaves ML	YL	LB	OB	LX	Petiole MP	YP	XP	Reproductive FB	FL	FR	Other ST	GU	BA	HE	HS	GS	EA	Invert. XI	Le	Ce	X
Pterocarpus m.	1	36.6	36.6																					
Anogeissus l.	2	13.6	13.2			0.1								0.1										0.1
Bauhinia r.	3	11.5	11.2											0.3										
Saccopetalum t.	4	6.5	6.3											0.1										
Shorea r.	5	5.5				4.1																		1.5
Terminalia t.	6	4.4	3.6					0.5																0.3
Madhuca i.	7	3.7												3.7										
Terminalia c.	8	3.4	1.5					2.0																
Lannea c.	9	2.6	2.5												0.1									
Emblica o.	10	2.1	2.1																					
Ficus t.	11	1.8											1.5	0.1										0.3
Holarrhena a.	12	1.2	0.7					0.4								0.1								
Bombax c.	13	1.1						1.1																
Zizyphus x.	14	0.9	0.9																					
Albizzia o.	15	0.3											0.3											
Other tree spp (8)		1.4	0.3										0.5	0.3										0.2
Other ground		3.3	0.3											0.3			0.3			0.7				1.8
TOTAL			79.3			4.2		4.0					2.2	4.9	0.1	0.1	0.3			0.7				4.2

TABLE 9.C (Contd.) MONTHLY FEEDING BUDGETS.

JANUARY 1982: N=513

Species	Rank	Total	Percentage of feeding records																				
			Leaves					Petiole			Reproductive			Other							Invert.		
			ML	YL	LB	OB	LX	MP	YP	XP	FB	FL	FR	ST	GU	BA	HE	HS	GS	EA	XI	Le	Ce	X
Pterocarpus m.	1	23.6	23.6																					
Shorea r.	2	22.2			1.4	12.1																		8.8
Bauhinia r.	3	10.9	10.3					0.2						0.4										
Ficus i.	4	9.9			9.9																			
Saccopetalum t.	5	4.3	4.3																					
Emblica o.	6	3.5	3.5																					
Anogeissus l.	6	3.5	3.5																					
Terminalia t.	7	3.3	2.9											0.4										
Terminalia c.	8	2.7	1.0					1.8																
Holarrhena a.	9	2.5	2.1													0.2						0.2		
Syzygium c.	9	2.5			1.2	1.0																		0.4
Cordia l.	10	1.4	1.4																					
Ehretia l.	11	1.0									0.8													0.2
Terminalia b.	12	0.8	0.2											0.6										
Butea m.	13	0.4																						0.4
Other tree spp (8)		2.2	0.4			0.4							0.2	0.4	0.2							0.2		0.4
Other ground		5.3		0.2		0.4											2.1	0.2		0.8				1.6
TOTAL			53.2	0.2	12.5	13.8		1.9			0.8		0.2	1.8	0.2	0.2	2.1	0.2		0.8		0.4		11.7

TABLE 9.C (Contd.) MONTHLY FEEDING BUDGETS.

FEBRUARY 1982: N=502

Species	Rank	Total	Percentage of feeding records																				
			Leaves					Petiole			Reproductive			Other							Invert.			
			ML	YL	LB	OB	LX	MP	YP	XP	FB	FL	FR	ST	GU	BA	HE	HS	GS	EA	XI	Le	Ce	X
<u>Bauhinia r.</u>	1	18.5	18.5																					
<u>Shorea r.</u>	2	15.3			0.6	8.0					2.6													4.2
<u>Syzygium c.</u>	3	10.2		0.2	1.8	4.8															0.4			3.0
<u>Ficus i.</u>	4	8.0		0.4	1.8	3.2							1.8											0.8
<u>Ficus t.</u>	5	6.8	0.2										6.6											
<u>Ehretia l.</u>	6	6.6				0.4					6.2													
<u>Saccopetalum t.</u>	7	4.0	3.8																					0.2
<u>Bombax c.</u>	8	3.2									3.2													
<u>Pterocarpus m.</u>	8	3.2	3.2																					
<u>Butea m.</u>	9	2.4									2.4													
<u>Ougenia d.</u>	10	2.2									2.2													
<u>Terminalia t.</u>	10	2.2	2.2																					
<u>Holarrhena a.</u>	11	2.0														2.0								
<u>Litsea s.</u>	12	1.4	1.4																					
<u>Anogeissus l.</u>	13	1.2	1.2																					
Other tree spp.(14)		7.0	3.0		0.4	2.0		0.2			0.4				0.2									
Other ground		6.0															2.6			0.4				3.0
TOTAL			33.5	0.6	4.6	18.3		0.2			16.9		8.8		0.2	2.0	2.6			0.4	0.4			11.6

TABLE 9.C (Contd.) MONTHLY FEEDING BUDGETS.

MARCH 1982: N=504

Species	Rank	Total	Percentage of feeding records: Leaves					Petiole			Reproductive			Other							Invert.			
			ML	YL	LB	OB	LX	MP	YP	XP	FB	FL	FR	ST	GU	BA	HE	HS	GS	EA	XI	Le	Ce	X
Shorea r.	1	38.9									30.8	6.0												2.2
Ougenia d.	2	12.5				0.2					0.2	11.1												1.0
Syzygium c.	3	11.9		0.2		9.5																		2.2
Madhuca i.	4	8.3									8.3													
Ficus i.	5	3.8			1.4	1.2							0.2											1.0
Albizzia o.	6	3.6			2.6	1.0																		
Ehretia l.	6	3.6				1.8					0.8	0.4												0.6
Mallotus p.	7	3.4				3.0																		0.4
Butea m.	8	2.0									1.6													0.4
Careya a.	9	1.8			1.2	0.2																		0.4
Schleichera o.	9	1.8				1.0					0.8													
Bauhinia m.	10	1.4											1.4											
Cordia l.	11	1.2	1.2																					
Ficus p.	12	1.0											0.8											0.2
Sterculia u.	13	0.2													0.2									
Other tree spp.(6)		1.2				0.4					0.2		0.2			0.2								0.2
Other ground		3.6	0.2																	0.8				2.6
TOTAL			1.4	0.2	5.2	18.3					42.7	17.5	2.6		0.2	0.2				0.8				11.1

TABLE 9.D. SUMMARY OF INTERMONTHLY VARIATION IN INDICES OF FEEDING BUDGETS.

						Diet overlap	
Month	% feed	H' spp	H' item	# trees	# spp	Item	Spp
APRIL	19.7	2.671	1.982	49.6	24	40.67	15.9
MAY	12.9	2.616	1.146	42.0	27	40.28	19.3
JUNE	12.6	2.134	0.975	41.2	22	42.12	17.1
JULY	22.4	2.905	2.068	50.2	34	45.48	21.0
AUGUST	27.4	2.572	1.794	60.4	27	53.87	22.4
SEPTEMBER	29.9	2.848	1.807	48.0	30	54.38	30.5
OCTOBER	42.6	1.724	1.191	31.0	24	48.46	21.4
NOVEMBER	42.8	2.314	1.161	34.0	22	52.63	32.3
DECEMBER	38.6	2.209	0.877	28.8	21	43.51	32.0
JANUARY	23.1	2.359	1.508	33.0	22	48.85	30.5
FEBRUARY	19.2	2.716	1.855	43.2	28	51.50	26.0
MARCH	17.5	2.151	1.607	48.8	18	31.50	15.0
MEAN	25.7	2.435	1.498	42.5	24.9	46.10	23.62
± S.D.	10.7	0.347	0.413	9.5	4.4	6.83	6.43

Abbreviations:

% feed = Number of feeding records as a percentage of total number of records collected per month.

H' spp = Shannon-Wiener index of diversity for species & item feeding budget.

H' item = " " " " " " item feeding budget.

tree = mean number of trees troop fed in per day.

spp = mean number of tree species fed in per day.

Overlap

Item = mean percentage overlap of month with other 11 months by food items.

Spp = " " " " " " " " " " food items and species.

TABLE 9.E. PERCENTAGE UTILIZATION BY LANGURS OF GUM, BY TREE SPECIES AND SITE OF ORIGIN.

SITE		TREE SPECIES Percentage of observations.											
		Lc	Su	Bl	Al	Cl	Cm	Tb	Tt	Pm	Lp	Total	N
	Hole	14.3		60.6								15.8	49
	Cleft	26.6		6.1	6.3					100		18.7	58
A	Branch loss	15.8	4.5		12.5							11.6	36
	Branch damage			3.0			20					0.6	2
	Bole	5.4	15.9		50.0	16.7						8.7	27
	Primary branch	1.5	27.3			16.7	20					5.5	17
	Secondary branch		20.5	6.1			40					4.2	13
B	Primary/Secondary Junction	1.5										0.9	3
	Terminals	1.0	25.0	24.2	18.8		20.0	100	100			8.7	27
	Leaf tip										100		2
	Stalagmite	17.2										11.3	35
	Woodpecker hole	3.5										2.3	7
	Chital antler gouges				12.5							0.6	2
C	Nail wound	0.5										0.3	1
	Elephant damage	0.5										0.3	1
	Baiga axe cuts					66.7						1.3	4
	Gleaning	1.0										0.6	2
	Unknown	11.3	6.8									8.4	26
Total		203	44	33	16	6	5	1	1		1		310

A = major natural damage, B = minor damage, pore sites, leaf tips, C = animal induced sites.
Lc = Lannea coramandelica, Su = Sterculia urens, Bl = Buchanania lanzan, Al = Anogeissus latifolia.
Cl = Cordia latifolia, Cm = Cordia myxa, Tb = Terminalia balerica, Tt = Terminalia tomemtosa.
Pm = Pterocarpus marsupium, Lp = Lagerstroemia parviflora.

TABLE 9.F SUMMARY OF SOME CERCOPITHECID DIETS.
(Abbreviations as in Table 9.A)

SPECIES	LOCATION	DIET ML	YL	OLB/LB	FL/FB	FR	INVERT.	SOURCE
Colobinae								
Colobus badius	Tana	11.5	36	16.4	6.2	25	–	Marsh (1981c)
	Gombe	44.1	32	2.8	6.8	11.4	–	
	Kibale	23.1	39.4	11.2	11.9	5.7	–	
	Fathala	5.4	24.0	17.5	8.7	35.9	–	
C. guereza	Kibale	12.4	57.7	4.0	2.1	13.6	–	Oates (1977a)
C. satanas	Cameroon	19	18	?	5	58	–	McKey (1978)
Presbytis entellus	Kanha	34.9	3.6	10.7	9.5	24.5	2.8	this study
	Singur	54		5	37	–		Oppenheimer (1978)
	Polonnaruwa	21	27	?	7	45	–	Hladik (1977)
P. senex	"	40	20	?	12	28	–	Hladik (1977)
P. johnii	Kakachi	20.3	25.5	5.7	9.3	25.1	–	Oates *et al* (1980)
P. obscura	Krau	22	36	?	7	35	–	Curtin (1980)
P. melalophus	Krau	11	24	?	6	56	–	Curtin (1980)
Cercopithecinae.								
Cercopithecus ascanius	Kibale		16.1		15.3	43.6	21.8	Struhsaker (1980)
C. sabaeus	Assirik		?		13	63	13.1	Harrison (1983c)
C. mitis	Kibale	6.8	9.5	2.8	11.8	43.1	19.8	Rudran (1978)
Cercocebus albigena	Kibale	–	3.4	1.1	3.4	58.8	26.0	Waser (1977a)

CHAPTER 10

ECOLOGICAL INTER-RELATIONSHIPS

CHAPTER 10 ECOLOGICAL INTER-RELATIONSHIPS.

10.1 INTRODUCTION.

In this final chapter an attempt is made to integrate some aspects of langur activity, ranging and feeding patterns to look for significant inter-relationships and to try and tease cause from effect.

A major aim of field primatology has been to generate and test hypotheses seeking to explain the relationship, if any, between habitat, social organisation and ecology. The adaptive significance of the enormous range of primate social structure, both within and between species, and the importance of phylogenetic inheritance is still not clear, but understanding has increased considerably since the speculation began. This understanding has accumulated through a series of theoretical and field work papers, many of which are found in Sussman (1979). With the acquisition of further field studies, the emphasis in the early papers on gross differences in feeding ecology and habitat (Crook & Gartlan 1966, Jolly 1972, Crook 1970, Eisenberg et al 1972) has been replaced by a realisation that finer ecological differences are important (Clutton-Brock 1974a, Hladik 1977, Clutton-Brock & Harvey 1976,1977). The early reviews correlated 'grades' of diet and habitat with social structure but the expansion of field studies subsequently brought such broad relationships into question; in particular by documenting the natural history of previously unstudied rainforest primates. It was noted that phylogenetic inheritance is likely to restrain possible adaptation and that gross habitat types such as 'forest' encompass a multitude of different environments, differing widely in structure and in the spatial and temporal distribution of food resources. Diet distinctions, such as frugivore or folivore also include much potential variation. At the other side of the equation it was noted that similar broad categories of social structure may, although superficially equivalent, be very disparate with respect to social change and selective pressures acting on individuals to form societies. For example, multimale groups in langurs, gorillas and lemurs may diverge widely in detail and have arisen for quite different reasons.

With the shift in emphasis from gross to fine distinctions the focus of fieldwork on terrestial savannah primates gave way to more studies on arboreal forest monkeys and apes. The 'fine' approach can be illustrated by Clutton-Brock's (1974a) hypothesis linking differences between sympatric red and black & white colobus social organisation with the spatial and temporal distribution of food trees and the quality of the diet. On a larger scale the 'grade' approach of Crook & Gartlan (1966) has been expanded into a more objective continuum by Milton & May (1976) and Clutton-Brock & Harvey (1977). They examined correlations between variables such as range size, density, sex ratio and diet type over a large range of species. For example, body weight was found to be larger for folivores than frugivores, range size was related to group weight and monogamy was largely restricted to territorial species living at low density. Sex ratio differences and the unimale-multimale distinction defied explanation.

Recently, investigations have more specifically attempted to unravel the relationship between ranging patterns, diet and habitat. Such information may also indicate the adaptive significance of different social structures (Marsh 1981b,McKey & Waterman 1982). These studies have usually employed a grid system in which the animals are sampled for a run of dawn to dusk follows every month, for a year, using scan recording (e.g Clutton-Brock 1972, Struhsaker 1975, Waser 1977a, Marsh 1978, McKey & Waterman 1982, Oates 1977a, Harrison 1983a).

Intuitively, food would seem likely to be important in determining ranging patterns; three main types of methodology have been used to test for any relationship (Marsh 1981b). Firstly, spatial variation in food sources has been analysed with respect to the annual group ranging pattern e.g. Clutton-Brock (1975b), Marsh (1981b), Harrison (1983a). Secondly, association between temporal variation in diet and food availability has been tested for e.g. Marsh (1981b), Struhsaker (1974), Harrison (1983a). Thirdly, intra-specific variation in ranging, feeding and habitat has been compared between groups e.g. Richard (1977), Freeland (1979), Marsh (1981b). Food is not the only, nor nessarily the most important determinant of ranging pattern. Factors such as other groups (Struhsaker 1975), water (Altmann & Altmann 1970,Harrison 1983a), predators (Altmann & Altmann 1970), disease (Freeland 1979,Coelho et al 1977), weather (Chivers 1974,McKey & Waterman 1983), sleeping sites (Harrison 1983a) and habitat stucture (Gautier-Hion et al 1981) have been implicated as determinants of ranging patterns for a wide variety of primates. What are the important variables for langurs ? Here, temporal and spatial variation in troop diet, vegetation, inter-group relations and ranging will be explored, looking for biologically significant relationships. Correlates of intra-specific variation at the level of populations or groups, as exemplified by red colobus (Marsh 1978) cannot be examined in langurs, as the ecological data are not available. Previous langur research has concentrated on social structure, reviewed in Chapter 6, but was carried out without concurrent examination of ecology. Inter-colobine variation is briefly discussed in each chapter but detailed analysis is beyond the scope of this study. However, such investigation may be premature; out of some 24 extant colobines, there appear to be comparable detailed studies using grids and scan sampling for only six and six species remain almost totally unknown.

A recurring hypothesis in primate ecology has been the prediction that both large group and range sizes are associated with clumped, temporally and spatially variable food sources (Chalmers 1979). Ephemeral items such as 'flush' and reproductive plant parts tend to be available for brief periods and occur in clumps, widely dispersed through the forest. Sufficient food can only be harvested by a widespread and diverse ranging pattern. In contrast, when feeding on items such as mature leaf the food supply is omnipresent and available throughout most of the year. A widespread diverse, ranging pattern would be not be required and would result in higher energy costs, which may be especially important when feeding on such a low energy content food. Similar considerations predict that for foragers of ephemeral items it should be most advantageous to live in large groups, whereas exploiters of adundant, predictable items should form smaller aggregations (Clutton-Brock 1974a,1975b, Chalmers 1979). Examples of inter-specific and intra-specific variation in agreement with these predictions are known for Asiatic and African colobines and Malagasy lemurs (Clutton-Brock 1974a,1975b, Hladik 1975,Sussman 1977). Similar associations between social organisation and diet have been documented for grazing and browsing African ungulates and graminivorous and insectivorous birds (Clutton-Brock 1974a). If such a relationship is applicable for Kanha langurs, we would predict that range size would be smaller when feeding on mature leaf than when foraging on 'flush' and reproductive plant parts.

10.2 METHODS.

The data used in this chapter are taken from the relevant preceeding chapters: climate (Ch.3), vegetation structure and phenology (Ch.5), activity (Ch.7), ranging patterns and inter-group encounters

(Ch.8) and feeding budgets (Ch.9). All the data used in 10.4 will be found in the appropriate chapter or Appendix V. The discussion is considered in the same section as the results. The biological significance of relationships, tested by Spearman rank correlation coefficients, are discussed and the probable direction of cause and effect considered. Considerable care has to be exercised when imputing causality from such analysis (Sokal & Rohlf 1969) and it can only be tentative and speculative. The confirmation or otherwise of these associations will have to await the collection of comparable inter-population data.

10.3 SPATIAL VARIATION.

In Chapter 9 temporal variation in the consumption of certain dietary items was found to be closely related to their availability. We might also predict that the differential use of quadrats is related to spatial variation in food source distribution. Using the total enumeration of trees per quadrat in "C"'s annual range (see Chapter 5) and quadrat utilization for the twelve months combined (see Chapter 8), this relationship can be tested by a method developed by Clutton-Brock (1972,1975b) and Marsh (1981b). Correlation coefficients were used to test for the association between the % of occupancy records per quadrat and the area at breast height (hereafter 'ABH') for each tree species, for each quadrat. Two sets of tree species were used: a/ the top ten tree species ranks in the annual budget in terms of feeding time and b/ the top ten species ranks in the annual budget in terms of selection ratio (see Chapter 9). The correlation coefficients for each set of trees are tabulated below :

Rank	a/ Feeding time rank: Species	r_s	b/ Selection ratio rank: Species	r_s
1	Pterocarpus m.	0.212**	Anogeissus l.	0.268**
2	Shorea r.	0.264**	Bauhinia r.	0.281**
3	Bauhinia r.	0.281**	Ehretia l.	0.139
4	Anogeissus l.	0.268**	Pterocarpus m.	0.212**
5	Saccopetalum t.	0.184**	Ficus a.	0.186**
6	Emblica o.	0.376**	Emblica o.	0.376**
7	Terminalia c.	0.160	Saccopetalum t.	0.184**
8	Syzygium c.	0.253**	Madhuca i.	0.192**
9	Ficus a.	0.186**	Lannea c.	0.201**
10	Lannea c.	0.201**	Terminalia t.	0.221**

[** = $p<0.01$, N=255]

Quadrat utilization was significantly and positively correlated with the abundance of nine of the feeding time species set and also with nine of the selection ratio set (seven species were shared between the two sets). The strongest relationships were with the abundance of Emblica and Bauhinia retusa. However, there may have been considerable inter-correlation amongst these trees, especially those which tended to clump about the chattan (see Chapter 5). It is therefore possible that many of the above correlations are spurious if langur ranging pattern was strongly determined by one species, which happened to be associated with others. However, none of the correlation coefficients calculated between the trees in b/ above were significant ($P>0.05$). A multiple regression analysis (Snedecor & Cochran 1967) was run on MINITAB (Ryan et al 1981) with quadrat occupancy as the dependent variable and ten independent variables- the ABH per quadrat for the top ranking species by selection ratio (set b/ above). The regression was significant ($F=42.29, df=10$ & $214, p<0.01$) and explained 66.4 % of variability in quadrat use. The first variable selected was Anogeissus ($b_i=0.0172, t=4.75, p<0.001$), accounting for 24.78 % of variation in range occupancy. Significant partial regression coefficients were found for all species except Ehretia. Together Anogeissus and Bauhinia retusa explained 40.3 % of variation. Therefore, the multiple regression confirms the results of the original correlation analysis and the order of importance of tree species in explaining quadrat occupancy was similar between the two methods. It suggests that all of the tree species with high selection ratios, apart from Ehretia, are related to langur ranging pattern independently of each other.

It is also possible that range utilization was related to the lumped frequency of occurrence of food trees (Clutton-Brock 1972, Marsh 1981b). To test for this, the correlation coefficient between range occupancy and the ABH for the top rank species was calculated and then for species successively combined in descending rank order. Both tree sets a/ and b/ ranked on importance in terms of feeding time and selection ratio were used. The coefficient for the cumulative combined abundances of tree species is shown in Fig 10.1. For the set of trees ranked by feeding time, utilization was significantly related to the lumped frequency of all cumulative combinations of tree species with, after the addition of three species, a very gradual increase in r_s. Range utilization was also significantly correlated with accumulated tree abundance when species were ordered by descending selection ratios. The relationship was stronger than for the set ranked by feeding time and the rate of increase in r_s with the accumulation of species was higher.

The above analysis provides evidence that the intensity of use of the annual range by langurs was related to the distribution of food sources. Furthermore, the relationship was stronger for the highly selected species than for those most fed upon. It is possible however, that such relationships could arise simply by the animals selecting quadrats with abundant tree growth as found for red colobus by Marsh (1981b). To examine this relationship, quadrat utilization was tested against the total ABH for all species (50) per quadrat. A significant correlation was found (r_s=0.340,df=253,p<0.01). This suggests, as shown in 8.3.2 that langurs select for forest and against meadow quadrats. The substantially higher coefficient for the correlation of range use with the distribution of the top 10 species, in terms of selection ratio, as opposed to all species combined suggests that ranging patterns were related to the distribution of these species rather than to the forest as a whole. The consistently lower coefficient for species, important in terms of feeding time, than the coefficient for species important in terms of selection ratio suggests that of the food trees those highly selected for are the most important in influencing ranging patterns.

A complication, noted by Clutton-Brock (1972), is that the above result could be interpreted in at least two ways :

a/ the distribution of trees determined the pattern of range use.

b/ the pattern of range use was determined by another factor and the troop fed heavily on the trees present in those quadrats occupied.

If "C" troop preferred the chattan quadrats (see 8.3.2) for reasons unconnected with food (such as predation risk, water or sleeping site availability) and fed on trees which were within them we would expect selection ratios within such quadrats to be inconsistent and dissimilar to ratios calculated across the entire annual range (Clutton-Brock 1972,1975b). This relationship can be tested for using the method of Clutton-Brock (1972) in which the rank of species selection ratios (see 9.3.3) within quadrats is examined. For the top ten species, ranked in descending order of importance of selection ratio calculated across the annual range (hereafter 'range selection ratios'), the selection ratios were estimated for each quadrat (hereafter 'quadrat selection ratios'), except those negatively numbered. This was achieved by dividing the number of feeding records for each species in each quadrat by the ABH for each species in each quadrat. In the matrix of Table 10.A species are ranked in descending order of range selection ratios. In a/ the number of quadrats in which the quadrat selection ratio of $species_x$ exceeded the quadrat selection ratio of $species_y$ (when both species present in the quadrat) is tabulated. In b/ the number of quadrats is shown in which the quadrat selection ratio of $species_y$ exceeded that of $species_x$ (when both species present in the quadrat). For example, in two quadrats the Anogeissus quadrat selection ratio exceeded that of Bauhinia and in one quadrat the same measure for Bauhinia exceeded that of Anogeissus.

As Clutton-Brock (1972) states, if range selection ratios were not consistent within quadrats, the quadrat selection ratio for each species would be expected to exceed that of other species in as many quadrats as it was exceeded by each species. Examination of Table 10.A suggests that species with high ranking range selection ratios consistently exceeded the quadrat selection ratios of lower ranking species more frequently than they were exceeded i.e. high ranking species 'won' more frequently than they 'lost'. Therefore, quadrat selection ratios were consistently ranked in a similar order to range selection ratios, supporting the hypothesis that the distribution of food sources determined, in large part, ranging patterns.

Clutton-Brock (1972) found a similar association to that found here, between the spatial distribution of food trees in a Tanzanian forest and red colobus range use. Quadrat utilization was not significantly related to the abundance of any of the top ten food tree species (ranked in order of feeding time investment) when considered separately. Range use was, however, closely related to the lumped frequency of the top three species ranks. With the accumulation of successively less important species the correlation disappeared. Clutton-Brock (1972) also showed that, as here, animals selected food species in approximately the same order, within quadrats as they did across the entire range. Marsh (1981b) found that quadrat utilization by Tana red colobus was significantly correlated with quadrat-specific tree abundance for the top 2,3 and 4 ranks in the feeding budget. However, a strong significant correlation was also found between range use and the spatial distribution of all trees, whether food-providers or not. Marsh concluded that, at least for the most intensively used area of the range, utilization was related to the distribution of important food species but over the entire range, particular species may be less important than the rest of the species combined.

The two red colobus studies and the observations of Kanha langurs suggest a causal relationship between the spatial distribution of important food trees and ranging patterns. Additionally, this study suggests that the distribution of highly selected species is more closely related to ranging behaviour than the distribution of trees fed upon the most.

10.4 TEMPORAL VARIATION.

In this section seasonal variation in ranging behaviour will be examined with respect to temporal variation in diet, activity and weather. In 9.3.4. it was shown that the consumption of fruit, flowers, flowerbuds and open leaf buds was probably related to their availability. In this exploratory analysis Spearman rank correlation coefficients were calculated for a selection of pertinent variables; a matrix of the coefficients is shown in Table 10.B using data extracted from Chapters 3,7,8,9. The actual values of significant ($p<0.05$) correlations included in the table have been omitted from the text, for the sake of clarity. A statement of a 'significant' relationship indicates statistical significance at the level of 5%.

10.4.1 ACTIVITY, DIET AND WEATHER.

In Chapter 7, it was found that there was considerable inter-monthly variation in the proportion of time spent feeding, reaching a maximum in the winter. Intuitively, such variability may be related to diet composition, its quantity and quality. A significant positive relationship was found between the proportion of time spent feeding and the proportion of mature leaf in the diet (see Fig 10.2). Feeding time was significantly negatively correlated with leaf bud consumption and with young foliar and reproductive items combined (i.e.leafbuds,open leaf buds,young leaf,flower,flowerbud,fruit $r_s=0.664, p<0.05$) but not with any other individual plant part.

In comparison to leaf flush and reproductive items, mature leaves although abundant and proteinaceous, are energetically poor and costly to digest (Marsh 1978). Thus, langurs may be expected to spend more time feeding when mature leaf dominates the diet in order to eat sufficient to extract enough energy than when consuming energetically concentrated items such as fruit or 'flush'. Mature leaf may also require longer 'handling time', because it may need more mastication than less fibrous items. Thermoregulatory energy requirements are likely to be higher during the winter and monsoon months, owing to low night temperatures and wetting by rain.

Marsh (1981b) found a positive correlation between proportion of time spent feeding and the level of leaf buds, but not mature leaf, in the diet of Tana red colobus. Richard (1977) and Smith (1977) found that feeding time was negatively correlated with the proportion of mature leaves in the diet of lemurs (Propithecus verreauxi) and howler monkeys (Alouatta palliata) respectively. Milton (1980) noted a positive relationship, though not significant, between allocation of feeding time on leaf and proportion of time spent feeding in howlers. Therefore, associations are inconsistent between and within species.

In this study consumption of mature leaf was negatively correlated with temperature, probably as a result of 'flush' and reproductive parts being abundant during the hot weather months. Mature leaf was less available during this season (se Chapter 5) but still present in substantial quantities. The disproportionately low level of utilization suggests that 'flush' and reproductive items were 'preferred' items.

10.4.2 RANGING PATTERNS AND INTER-GROUP RELATIONSHIPS.

In Chapter 8 large seasonal variability was described in range size and frequency of inter-group encounters. The two measures are highly significantly positively correlated (see Fig 10.3).

Struhsaker (1974,1975) found a similar association between encounter rate and quadrat utilization diversity (H') in red colobus and concluded that inter-group relations determined ranging patterns since their diverse diet released them from the influence of food distribution. Clutton-Brock (1975b,1977b) considered that an alternative explanation is more likely; that ranging diversity, related to the spatial and temporal distribution of food sources, determines the frequency of encounters i.e. a reversal of cause and effect. Struhsaker (in Marsh 1981b) has, however, defended his conclusion with circumstantial evidence suggesting that encounters did have an independent influence on ranging patterns. Should encounter frequency in "C" troop be regarded as a cause or an effect of ranging patterns ? The association between the temporal and spatial distribution of food sources with ranging patterns suggests that encounter frequency may be a consequence of ranging behaviour. The circumstantial evidence that some conflicts may have occurred over particular highly selected trees (Chapter 8) also indicates that high encounter frequency arose from widespread ranging patterns. An exception may be April when, as described in Chapter 6, it is likely that the presence of infanticide-prone ("Q") males affected ranging behaviour. That the presence of predators may occasionally affect movements is suggested by the observation that the smallest daily range (13 quadrats) occurred when "B" troop was in the vicinity of an arboreal attack by a panther on a neighbouring troop.

In Chapter 8 a significant, negative association was noted between encounter frequency and the proportion of mature leaf in the diet. This was interpreted as support for Harrison's (1983a) hypothesis that encounter frequency and intensity should be related to the symmetry of distribution of important food sources between the opponents' ranges. Encounter frequency was also significantly negatively correlated with dietary species-specific item overlap i.e. encounters were common in months when the diet was unusual, largely as a result of feeding on ephemeral items. This association may have been a consequence of these unusual items being highly sought after and widely distributed, engendering larger range size and bringing the troop into greater conflict with other groups.

10.4.3.DIET COMPOSITION AND RANGING PATTERNS.

As mentioned in the Introduction an oft-repeated hypothesis has been that large range size is associated with temporally and spatially variable food sources. If applicable for Kanha langurs, range size would be predicted to be smaller when the diet is predominantly mature leaf than when consisting largely of 'flush' or reproductive items. The hypothesis is supported (see Fig 10.4); monthly range size is significantly negatively correlated with the proportion of mature leaf in the diet. Clutton-Brock (1974a) postulates that range size is small for animals feeding on mature foliage since a small patch of forest would provide sufficient of such a super-abundant resource. Small ranges may also be required in order to reduce energy expenditure as the diet may be energetically poor. However, a variation on this explanation may be more applicable to Kanha. In contrast to Gombe and Kibale, mature leaf sources were not evenly distributed about the forest but were clumped at Kuloo chattan, especially the two most important species for this item, Pterocarpus and Bauhinia retusa. The predominantly deciduous chattan vegetation provided most of the mature leaf whilst the sal forest provided little (see Chapter 9). Therefore, the small range, whilst feeding on mature leaf, may not have been a consequence of reducing energy expenditure but rather because, perhaps unusually, mature leaf was concentrated within a small area. If the troop were to increase range size when feeding on mature leaf only a few more food tree species and individuals would become available. Clutton-

Brock (1975b) found, similarly to this study, that Tanzanian red colobus moved shorter distances and ranged less diversely when the diet was predominantly mature leaf.

McKey & Waterman (1982) found a significant positive relationship between mature leaf consumption by black colobus and monthly range size. This inverted association did, however, owing to differences in resource distribution, support the essence of the Clutton-Brock (1974a) hypothesis. As discussed in Chapter 9, acceptable mature leaves at this Cameroon site were rare and widely dispersed in small clumps, because of the very high levels of secondary compounds in most species. Therefore, the spatial distribution of mature leaf was more similar to the pattern generally predicted for 'flush' or reproductive items and range size was large. When feeding on the preferred seeds and 'flush', which were seasonally abundant and occurred in large clumps, i.e. the generally predicted pattern for mature leaf, range size was small. Seasonally large range size may also have been a consequence of searching for scarce preferred items at the periphery of the range. A qualitatively similar relationship was reported for Himalayan langurs, by Sugiyama (1976 quoted in McKey & Waterman 1982), in which range size was small when feeding on abundant preferred items but when preferred items were scarce, range size increased.

The contrast between colobine diet-ranging relationships in Cameroon and central India emphasises the importance of fine distinctions. It also stresses that categories such as 'mature leaf' are human abstractions and leaf monkeys probably, in effect, perceive plant parts in terms of their temporal and spatial distributions and leaf chemistry and not as 'flat and leaf' or 'round and fruit', as perceived by human observers. Depending on leaf chemistry and vegetation structure 'mature leaf' may require foraging behaviour currently regarded as typical for overdispersed, clumped items such as fruit or vice versa. Perhaps the quantification of species-specific items in terms of their chemical content and dispersion in time and space, as opposed to irrelevant botanical classifications, such as 'mature leaf' would be helpful.

Ranging diversity (H') was significantly, positively related to the proportion of time spent on the ground (r_s=0.818,$p<0.01$). Perhaps this arose because an increase in ranging diversity resulted in the occupation of more meadow areas, thereby requiring more ground use. The inverse, that langurs are able to spend more time on the ground, due to some other factor such as low predation risk, and consequently range more diversely, is also possible. Ground use was significantly, negatively correlated to the index of clumping RU (r_s=-0.650,$p<0.05$); this may have been because less clumped range use (and clumping tended to be concentrated at Kuloo chattan) required more terrestrial movement.

RU was also significantly, positively associated with three measures of dietetic diversity: H' for species-specific items (see Fig 10.5), the number of trees fed in and the number of species consumed per month. These variables are significantly inter-correlated. Therefore, high diet diversity was associated with clumped patterns of range use. Inspection of Fig 8.5-10 suggests that most of the variation in clumping arises from variability in the degree to which "C" concentrated quadrat utilization at Kuloo chattan. That feeding diversity was related to the use of the chattan is supported by a significant negative relationship between item H' and species-specific item H' and RU with the proportion of time spent in sal forest (but not chattan) quadrats (r_s=-0.594,$p<0.05$; r_s=-0.699,$p<0.05$, r_s=-0.895,$p<0.001$, respectively). Therefore, when feeding in sal forest (little time was spent feeding on the meadows) diet diversity and degree of range clumping tended to be low. These relationships may result from higher tree diversity on the chattans than in the surrounding sal forest. With the demonstration that range use is correlated with the distribution of important tree species (see 10.3), it is possible that foraging for a highly diverse diet necessitates a high degree of range clumping at a patch of highly diverse forest. The inversion of cause and effect is also possible but less likely; i.e. that the clumping of range use was the result of some other factor and resulted in high feeding diversity.

Troop dispersion was significantly and positively correlated with the number of trees fed in per month and both item and species-specific item diet diversity i.e.the diet was more diverse when the troop was dispersed. Perhaps this arose as a result of a diverse diet requiring wide troop spread as food patches were small and dispersed. An alternative possibility, that troop dispersion was determined by some other factor, such as social behaviour, which influenced the diversity of feeding cannot be rejected.

In summary, speculating as to the direction of causality, it could be argued that mature leaves, owing to their particular chemistry, are not preferred food and that 'flush' and reproductive items are favoured when seasonally available. Because mature leaf is energetically poor and difficult to digest, despite the langurs' gut specializations, more time has to be invested in feeding than when harvesting more digestible, energy rich items. Fruit, flowers and 'flush' are only briefly available so that mature leaf tends to dominate the diet when they are not in season. As mature leaf sources are clumped at the chattan but the more ephemeral items dispersed through the forest, range size was smaller when the troop fed on mature foliage than when they fed on flush and reproductive items. Increased range size resulted in the troop coming into more frequent contact with other groups. Increased ranging diversity and reduced range clumping resulted in greater use of the ground as more meadow was necessarily occupied. The high diet diversity, achieved by feeding extensively on the diverse patch of forest at the chattan, resulted in pronounced clumping of range use.

10.5 CONCLUDING DISCUSSION.

This study has answered a few questions and posed many more. After many thousands of hours of watching langurs their social organisation is still poorly understood. The lack of detailed published information on the ecology and social organisation of all-male bands leaves a large gap in our understanding of this species. The adaptive significance of the unimale-multimale distinction appears intractable (see Chapter 6) but its elucidation may give greater understanding of social change, variation in social structure and infanticide.

Central Indian forests, in holding only one species of colobine and one of cercopithecine, will not be fertile stamping grounds for testing and developing hypothesis of inter-specific variation. However, because of the presence of a great range of relatively simple habitats, the region may be valuable for investigating the functional significance of intra-specific variation in sex ratios, group and range size and their relationship, if any, to the habitat. A further ill-understood aspect of langur biology is their digestive system and the consequences of possessing a cellulytic gut flora. Without information on nutritional requirements and the costs and benefits of foraging, it is difficult to interpret food choice in relation to leaf chemistry. If secondary compounds can be detoxified what is the physiological cost? Is dietary protein or that derived from the gut flora important ? The large seasonal variations in diet are likely to have profound consequences for the gut organisms and hence the host primate. In particular, the high insect intake could cause problems; in ruminants high protein,low fibre diets can cause bloat (West 1975). In comparison with the ruminant digestive system, prone to many disorders caused by dietary variations and forage poisons, the colobine system appears to be singulary robust (Chapter 9, Hladik 1977, Bauchop 1978). Perhaps the cellulytic gut flora can be switched off or bypassed ? The information on feeding, particulary the ingestion budgets of Hladik (1977), potentially allows the construction of natural food menus for captive animals, which with experimental manipulation, might be enlightening. With colobines showing a broad range of diets, it is possible that interspecific variation in gut physiology may be correlated with feeding patterns. The Hanuman langur is unusually variable in many aspects of its biology (Hrdy 1977b); it is possible that much of this adaptability arises from an unusually rugged digestive system which although permitting feeding on a stenophagous, mature leaf diet, does not require such, and therefore allows a seasonally diverse, euryphagous diet.

As alluded to in 10.4, it would seem likely that some of the lack of understanding of primate feeding arises from unrealistic categorization of food; i.e. bearing little relation to the way that it is actually perceived by leaf monkeys. For example, what has here been classed as the mature leaf of a certain species, should be more appropriately described in terms of the costs and benefits of consumption of beneficial and harmful (and synergistic) compounds, item density on the tree, spatial and temporal distribution and the animal's requirements. More detailed investigation of food items in relation to such variables may allow their categorization, preferably on a continuum, into more pertinent classes than the 'mature leaf of species x', when in some environments this item may have a dispersion equivalent to the expected distribution of say, fruit.

The presence of the chattan in "C" troop's range appeared to have important consequences. Its disproportionate use, the high diversity and density of food trees and evidence that it was defended against other troops suggested that it was an important resource. "C" troop may not, in this respect, have been 'typical' of Kanha langurs as few troops have access to a chattan. The distribution of these rocky outcrops may have important consequences for group dispersion, ranging patterns and inter-group relations. It is possible that those troops with access to a chattan attempt to orientate their range so as to include it in the centre, facilitating its defence. The mixed forest in the hills was similar, in species composition, to the chattan vegetation, but was not in proximity to sal forest. The study troop fed, seasonally, upon considerable quantities of food from the sal,particulary Shorea flowers and fruits. The absence of these seasonally super-abundant items in the hills is likely to have profound consequences for langur ranging and feeding behaviour. A study comparing hill mixed forest, unbroken sal forest without chattans and the chattan, meadow, sal forest mosaic of this study is likely to yield interesting comparisons.

An important problem of langur biology is to explain why Presbytis entellus is so widespread in terms of habitat and so tolerant of change when its Asiatic relatives are very restricted, habitat-specific and intolerant of change. If the entellus digestive system is important, how does it differ from other colobines? The unravelling of evolutionary relationships between the four Asiatic congeners, perhaps by biochemical techniques, might be illuminating. As the ancestor of Asiatic colobines, which immigrated from Africa, was necessarily semi-terrestrial, it may be that the Hanumun has retained characteristics of that adaptable animal whilst the golden, capped and Nilgiri langurs have evolved to cope with specialised evergreen habitats.

10.6 ECOLOGICAL INTER-RELATIONSHIPS : SUMMARY.

1/ The developement of hypotheses relating habitat to primate social organisation and ecology are briefly reviewed. It is predicted that troop range size would be smaller when feeding on mature leaf than when foraging on more spatially and temporally dispersed items.

2/ Annual quadrat utilization was significantly and positively correlated with the quadrat-specific dominance of 9 out of the 10 most important species in terms of feeding time in the annual budget and with 9 out of the 10 most important species in terms of annual selection ratio. The absence of significant inter-correlation between the spatial distribution of the tree species and a multiple regression supported the suggestion that food tree distribution determines the pattern of range use.

3/ Annual quadrat utilization was significantly and positively correlated with the accumulated tree abundance as successive tree species were combined in descending rank order of importance of annual selection ratios. The same relationship, though weaker, was found for species ranked in terms of feeding time.

4/ Whether the relationship between spatial distribution of food sources and ranging patterns could be legitimately regarded as causal or whether a third variable was involved was examined by calculating quadrat selection ratios. These were found to be ranked in a similar order to the annual range selection ratios, indicating consistency in species selection and hence supporting the hypothesis that the dispersion of highly selected species influences range utilization.

5/ Correlation coefficients were used to explore relationships in intermonthly variation between activity, diet and ranging patterns. The proportion of time spent feeding was significantly and positively correlated with the proportion of mature leaf in the diet, perhaps because of this items low energy yield and the prolonged mastication required.

6/ Range size was positively and significantly correlated with encounter rate and it was suggested that large range size brings "C" into increased contact with neighbours, rather than the alternative, that the presence of other groups influences ranging patterns. The negative correlation between species-specific item overlap and encounter rate was perhaps the result of wide ranging patterns, in search of an unusual diet, bringing the troop into contact with other groups more frequently.

7/ The prediction that range size should be negatively related to the proportion of mature leaf in the diet is supported. Range size is suggested to be function of the spatial and temporal distribution of different items, with parts such as mature leaf clumped at the chattan and flowers dispersed through the forest. It is stressed that species-specific item classification, as used here, may not be a particularly pertinent distinction relevant to primate foraging.

8/ A significant positive relationship between ground use and ranging diversity and a negative relationship between ground use and the degree of clumping of range use is interpreted as a result of the increased terrestriality required in order to occupy the meadow area.

9/ Diet diversity was significantly and positively associated with the degree of clumping of range use, probably arising from high food source diversity clumped on the island chattan. Diets dominated by mature leaf were similar to each other.

10/ Finally, it is suggested that the physiological ecology of gut flora and digestion, and the influence of chattan vegetation on feeding and ranging ecology would repay investigation. The classification of food items in terms closer to the langur perception of the costs and benefits of foraging, rather than our own, may be more realistic. The social structure, inter-group relations and ecology of the neglected all-male bands is a large gap in knowledge of langur biology. The elucidation of the functional significance of the unimale-multimale distinction might be the key to a more complete understanding of many aspects of langur social structure and social change.

FIG 10.1 VARIATION IN CORRELATION COEFFICIENT (r_s) BETWEEN QUADRAT SPECIFIC RANGE USE AND TREE ABUNDANCE WITH CUMULATIVE COMBINED NUMBER OF SPECIES (tree abundance = dominance (ABH))

N=255

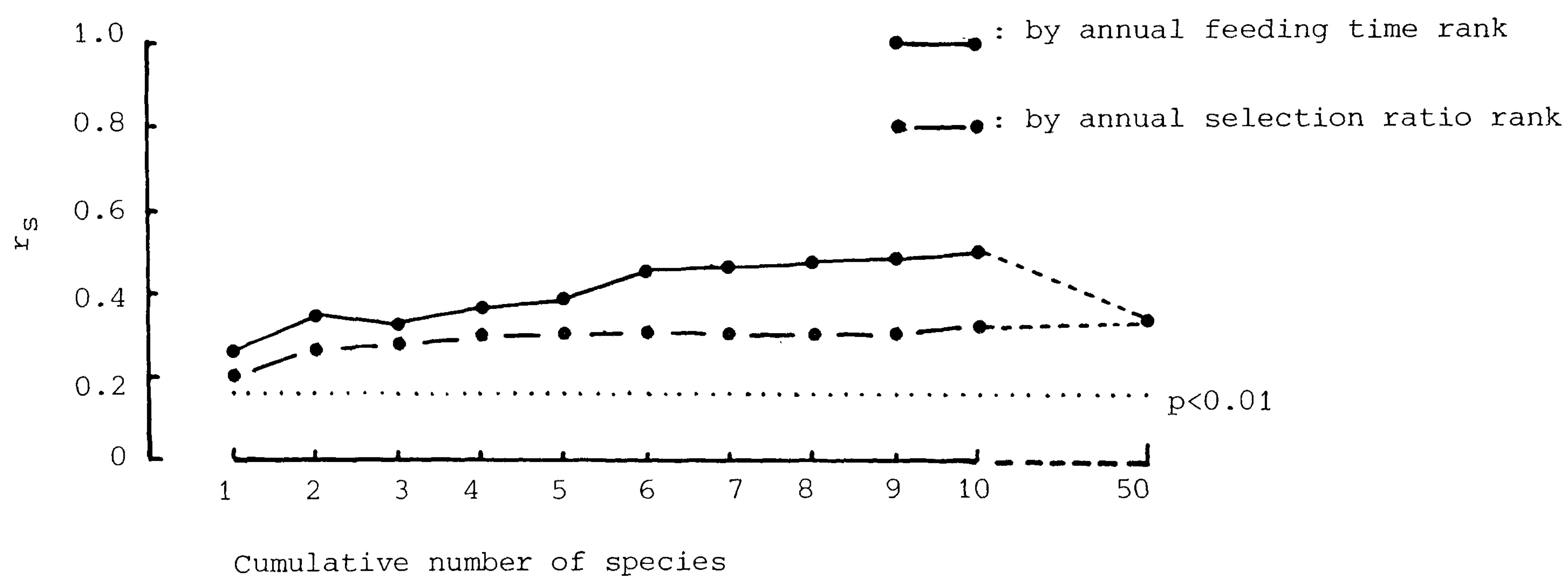


FIG 10.2 RELATIONSHIP BETWEEN % OF MATURE LEAF IN DIET AND % OF TIME SPENT FEEDING FOR 12 MONTHS. "C" TROOP.

$y=-19.66 + 1.926x$; $r_s=0.789$, n=12

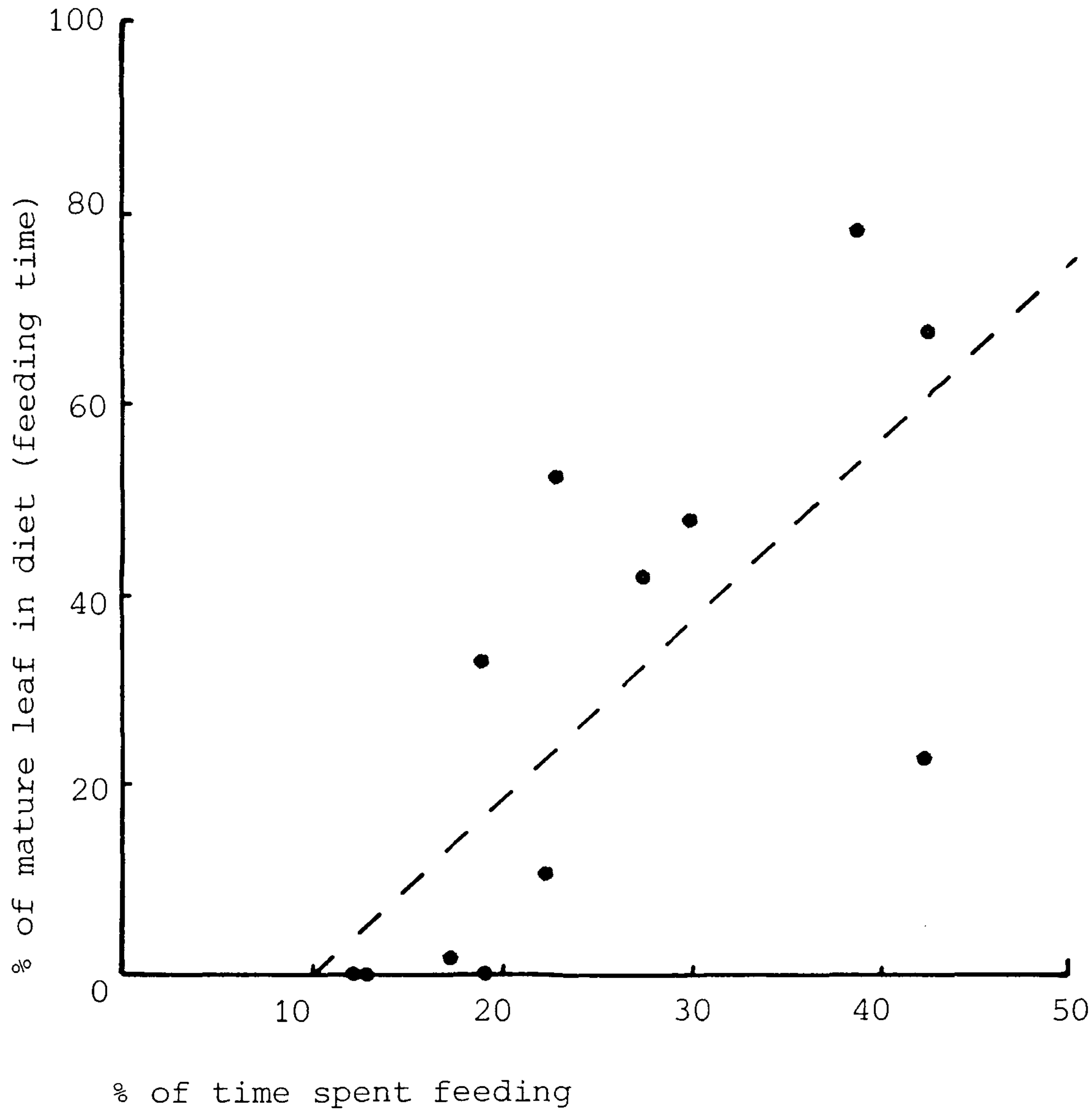


FIG 10.3 RELATIONSHIP BETWEEN NUMBER OF QUADRATS OCCUPIED PER MONTH AND ENCOUNTER FREQUENCY FOR 12 MONTHS. "C" TROOP.

$y=91.0 + 45.93x$; $r_s=0.831$, n=12

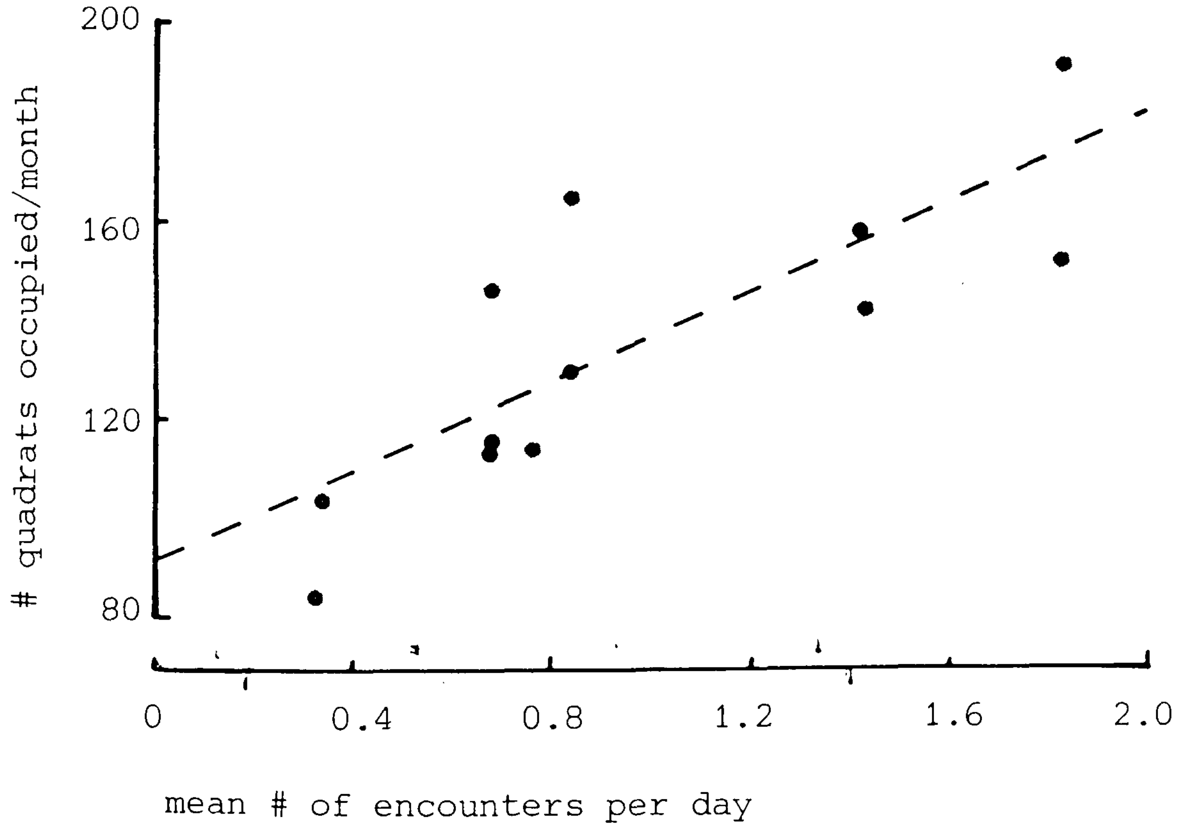


FIG 10.4 RELATIONSHIP BETWEEN % OF MATURE LEAF IN DIET AND NUMBER OF DIFFERENT QUADRATS OCCUPIED FOR 12 MONTHS."C" TROOP.

$y=131.42 - 0.750x$; $r_s=-0.758$, $n=12$

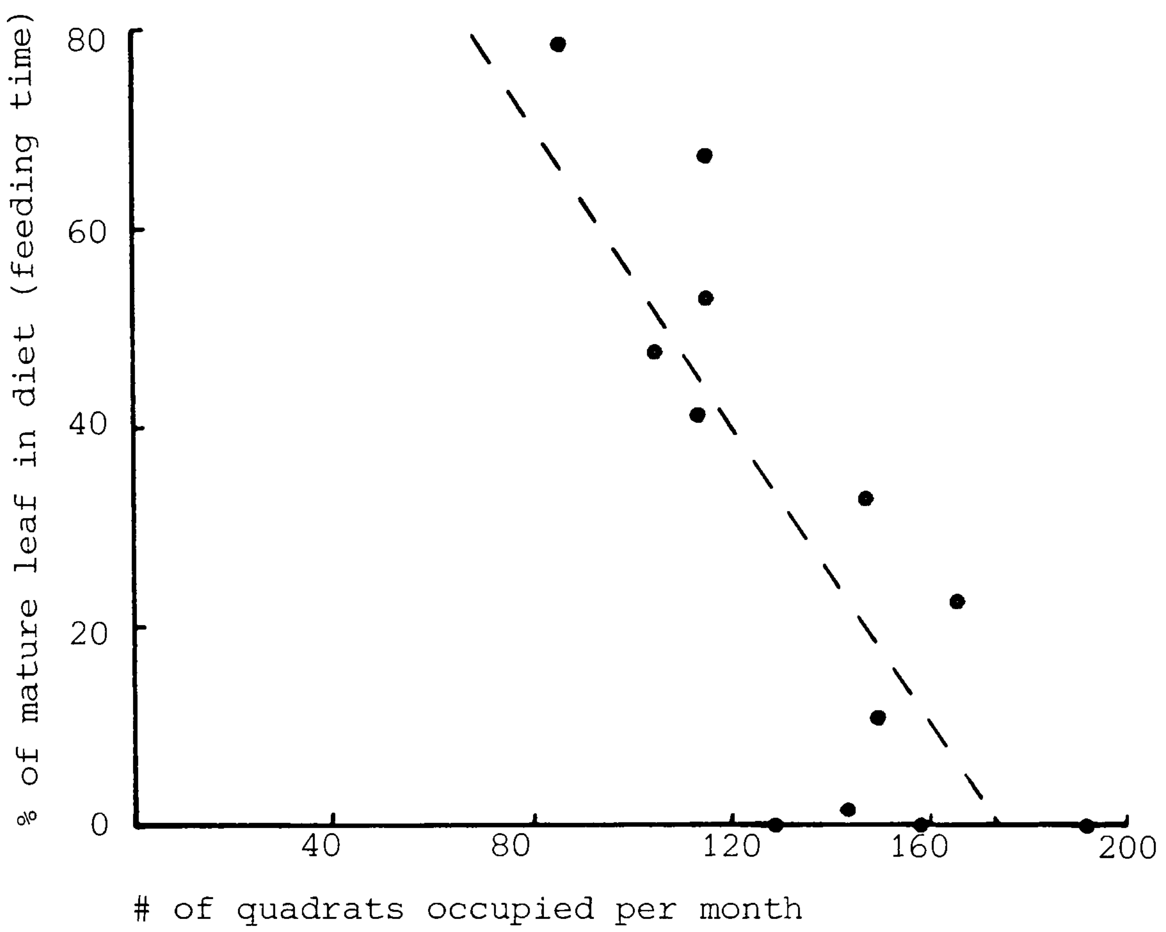


FIG 10.5 RELATIONSHIP BETWEEN DEGREE OF CLUMPING (RU) AND DIET SPECIES SPECIFIC ITEM DIVERSITY (H') FOR 12 MONTHS. "C" TROOP.

$y=0.413 + 0.388x$; $r_s=0.748$, $n=12$

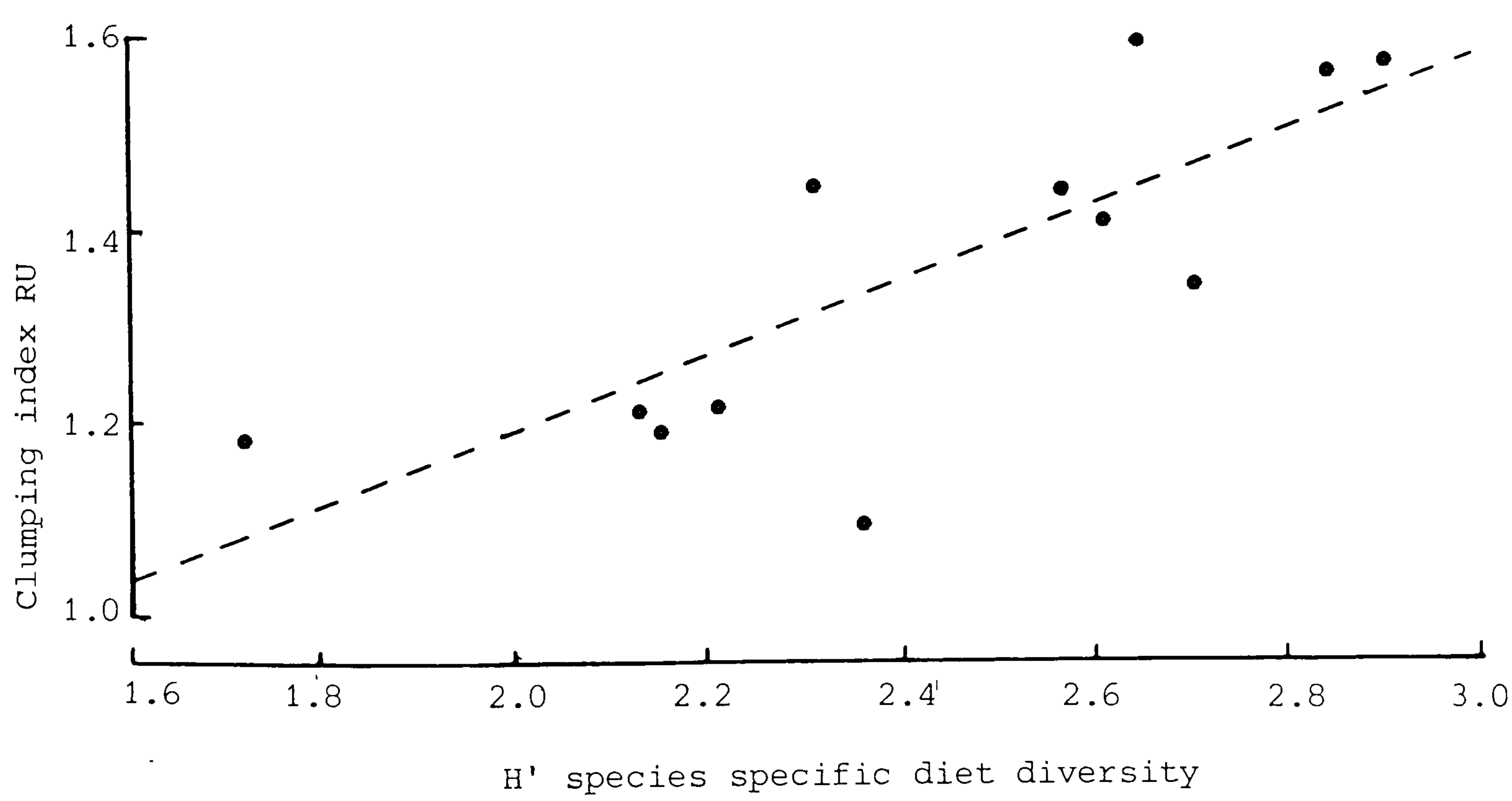


TABLE 10.A TEST OF CORRESPONDENCE BETWEEN RANGE SELECTION RATIOS AND QUADRAT SELECTION RATIOS.

A/ Number of quadrats in which $species_x$ quadrat selection ratio exceeds $species_y$, in which both present.

$Species_y$ \ $Species_x$	1	2	3	4	5	6	7	8	9	10
1 Anogeissus l.										
2 Bauhinia r.	2									
3 Ehretia l.	2	1								
4 Pterocarpus m.	1	5	0							
5 Ficus a.	1	1	1	2						
6 Emblica o.	4	4	3	5	0					
7 Saccopetalum t.	3	6	4	3	0	5				
8 Madhuca i.	0	1	1	2	0	4	8			
9 Lannea c.	4	3	4	2	2	5	7	0		
10 Terminalia t.	2	4	1	0	0	5	4	0	1	

B/ Number of quadrats in which $species_y$ quadrat selection ratio exceeds $species_x$, in which both present.

$Species_y$ \ $Species_x$	1	2	3	4	5	6	7	8	9	10
1 Anogeissus l.										
2 Bauhinia r.	1									
3 Ehretia l.	2	0								
4 Pterocarpus m.	1	0	0							
5 Ficus a.	1	0	1	0						
6 Emblica o.	2	3	2	2	3					
7 Saccopetalum m.	2	2	2	4	3	13				
8 Madhuca i.	0	0	0	1	1	1	2			
9 Lannea c.	3	1	1	1	2	1	1	1		
10 Terminalia t.	0	1	1	1	1	0	0	1	3	

TABLE 10.B CORRELATION MATRIX :RANGING,FEEDING AND ENVIRONMENTAL VARIABLES.
Spearman rank correlation coefficients r_s ,n = 12 (see text for details).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1 % FEED																						
2 % ML	0.789																					
3 % YL	-0.509	-0.689																				
4 % LB	-0.587	-0.504	-0.051																			
5 % OLB	-0.473	-0.236	-0.160	0.723																		
6 % FLB	-0.168	-0.173	-0.313	0.608	0.538																	
7 % FL	-0.508	-0.683	0.361	0.440	0.402	0.284																
8 % FR	-0.308	-0.669	0.818	-0.167	-0.424	-0.384	-0.141															
9 % INVERT	-0.570	-0.391	0.097	-0.603	-0.409	-0.256	-0.376	0.105														
10 # SPP/M	-0.028	-0.149	0.654	-0.308	-0.301	-0.034	0.000	0.410	0.543													
11 H' SPP	-0.105	-0.021	0.481	-0.131	0.074	-0.082	0.241	-0.028	0.312	0.802												
12 H' ITEM	-0.077	-0.183	0.288	0.145	0.242	0.485	0.354	-0.056	0.421	0.640	0.734											
13 SPP OVER	0.750	0.935	-0.473	-0.545	-0.277	-0.299	-0.750	-0.480	0.413	0.028	0.088	-0.228										
14 # TREE FED	-0.350	-0.416	0.547	0.007	0.077	0.175	0.449	-0.224	0.269	0.516	0.601	0.762	-0.480									
15 ENCOUNTER	-0.614	-0.814	0.488	0.449	0.325	0.011	0.591	0.518	-0.162	-0.041	-0.128	0.170	-0.822	0.291								
16 # Q/M	-0.473	-0.758	0.418	0.487	0.316	0.200	0.317	0.574	-0.122	0.064	-0.200	0.175	-0.682	0.095	0.831							
17 H' RANGE	-0.357	-0.408	0.025	0.558	0.326	0.511	-0.046	0.175	-0.036	0.088	-0.189	0.231	-0.399	-0.077	0.486	0.739						
18 RU	-0.049	-0.141	0.589	-0.334	-0.130	-0.134	0.345	-0.259	0.294	0.615	0.748	0.573	-0.046	0.678	-0.028	-0.102	-0.483					
19 DISPERSION	0.165	0.092	-0.265	-0.098	0.072	0.013	0.098	-0.074	0.469	0.418	0.620	0.722	0.077	0.637	0.025	-0.060	-0.200	0.729				
20 RANGE OVER	-0.294	0.092	0.218	-0.341	-0.168	0.034	0.175	0.049	0.222	0.368	0.371	0.301	-0.207	0.559	0.053	-0.238	-0.091	0.168	0.018			
21 RAIN	-0.236	-0.014	0.299	-0.391	-0.334	-0.420	-0.176	0.176	0.158	0.269	0.258	0.042	-0.014	0.279	0.100	-0.184	-0.106	0.141	0.210	0.653		
22 TEMP	-0.550	-0.843	0.627	0.312	-0.016	0.127	0.613	0.662	-0.382	-0.072	-0.028	0.035	-0.774	0.371	0.544	0.451	0.105	0.235	-0.088	0.025	-0.057	

KEY: Abbreviations will be found in Tables 8.A and 9.A,9.D except :
% FEED : % of daylight time spent feeding (see Chapter 7).
RAIN :total monthly rainfall (see Chapter 3).
TEMP :mean monthly maximum daily temperture (see Chapter 3).

Significance levels (df = 10):
$p < 0.05$: underlined
$p < 0.01$: bracketed
$p < 0.001$: boxed

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APPENDICES

APPENDIX 1 :TREES AND CLIMBERS RECORDED FROM KANHA TIGER RESERVE

PART 1

The species listed below were recorded from Kanha Tiger Reserve(Kisli,Kanha and Mukki Ranges),from identifications by Dr.P.C.Kotwal (M.P. Forest Dept.),Mr.A. Radcliffe-Smith (Royal Botanic Gardens,Kew) and P.N.Newton during 1980-82.

*=recorded from central Kanha meadows.
(C)=climber life form.
The vernacular names are those used by the Baiga forest tribe and in particular by Mungal and Mohan Baiga.The floras used were Brandis (1878,1906) and Witt (1916).The taxonomic order follows Heywood (1978)

FAMILY Binomial Synonyms	"VERNACULAR"
ANNONACEAE	
* Saccopetalum tomentosum H.f.& Th.	"KARI"
Uvaria tomentosa Roxb.	
LAURACEAE	
* Litsea polyantha Juss.	"MEDHAR"
Tetranthera monopetala Roxb.	
DIPTEROCARPACEAE	
* Shorea robusta Gaertn.	"SARAI","SAL"
Tetranthera monopetala Roxb.	
TILIACEAE	
* Grewia tiliaefolia Vahl.	"DHAMIN"
STERCULIACEAE	
* Sterculia urens Roxb.	"KULU"
* Sterculia villosa Roxb.	"KULU"
* Firmiana colorata (Roxb.)R.Br.	
Sterculia colorata Roxb.	
Sterculia wallichi Falc.	
BOMBACEACEA	
* Bombax ceiba L.	"SEMAL"
B.malabaricum DC.	
B.heptaphyllum Cav.	
Salmalia malabarica Schott & Endl.	
MALVACEAE	
* Kydia calycina Roxb.	"BARANGA"
K.fraterna Roxb.	
ULMACEAE	
* Holoptela integrifolia Planch.	"KARANJI"
Ulmus integrifolia Roxb.	
MORACEAE	
* Ficus bengalensis L.	"BAR","BANYAN"
F.indica Roxb.	

* Ficus religiosa L.		"PEEPUL"
* Ficus arnottiana Miq.		"SARIS PEEPUL"
* Ficus infectoria Roxb.		"PAKRI"
F.venosa		
F.lacov		
* Ficus cunia Ham.		"GHWI"
* Ficus glomerata Roxb.		"UMAR"
F.racemosa		
* Ficus parasitica Koenig.		"GUDSEE"
F.gibbosa Bl.,var parasitica King		
* Ficus tomentosa Roxb.		"BAR"

FLACOURTIACEAE

* Flacourtia ramontchi L'Herit		"KAITAR"
F.sapida Roxb.		
F.indica (Burm.f.)Merr		
* Casearia tomentosa Roxb.		"KUNDRU"
* Casearia graveolens Dalz.		"GIRCHI"
C.elliptica Willd.		

SAPOTACEAE

* Madhuca indica J.F.Gmel.		"MAHWA"
Bassia latifolia Roxb.		

EBENACEAE

* Diospyros melanoxylon Roxb.		"TENDU"

MYSINACEAE

* Embelia robusta Roxb.		"BAIBARANG"
E.Tsjeriam-cottam Wight		

MIMOSACEAE

* Albizzia odoratissima Benth.		"KURINGI"
Acacia odoratissima Willd.		
Mimosa odoratissima Roxb.		
* Acacia pennata Willd.	(C)	
Mimosa pennata Roxb.		

CAESALPINIACEAE

* Cassia fistula L.		"RELA"
Carthartocarpus fistula Pers.		
* Bauhinia racemosa Lam		"GUTARI"
B.parviflora Vahl.		
* Bauhinia malabarica Roxb.		"AMPTI"
Bauhinia variegata L.		"KACHNAR"
* Bauhinia retusa Ham.		"THAUR"
B.emarginata Royle		
* Bauhinia vahlii W.& A.	(C)	"MAHUL"

PAPILIONACEAE

* Ougenia dalbergioides Benth.		"TINSA"
Dalbergia oojeinensis Roxb.		
O.oojeinensis (Roxb.)Hochreut		
Milletia auriculata Baker	(C)	"GORALI"
Rubina macrophylla Roxb.		
* Butea monosperma Taub.		"PHARSA
B.frondosa Roxb.		
* Butea superba Roxb.	(C)	"BADOR PHARSA
* Dalbergia paniculata Benth.		"MAULA"

* <u>Pterocarpus marsupium</u> Roxb.	"BIJA"
* <u>Erythrina suberosa</u> Roxb.	"HARUWA"
LYTHRACEAE	
* <u>Lagerstroemia parviflora</u> Roxb.	"LEDIA"
* <u>Woodfordia fruticosa</u> (L.)Kurz	"SURTELI"
<u>W.floribunda</u> Salisb.	
MYRTACEAE	
* <u>Syzygium cumini</u> (L.)Skeels	"JAMUN"
<u>S.jambolanum</u> W.&A.	
<u>Eugenia jambolana</u> Lam.	
* <u>Careya arborea</u> Roxb.	"KHUMBHI"
ANACARDIACEAE	
* <u>Mangifera indica</u> L.	"AM"
* <u>Buchanania lanzan</u> Spreng	"CHAR"
<u>B.latifolia</u> Roxb.	
* <u>Lannea coramandelica</u> (Houtt.)Merr	"GHARRI"
<u>Odina wodier</u> Roxb.	
<u>L.grandis</u> Engl.	
* <u>Semecarpus anacardium</u> L.f.	"BHILWA"
MELIACEAE	
* <u>Azadirachta indica</u> A.Juss.	"NEEM"
<u>Melia azadirachta</u> L.	
<u>M.indica</u> A.Juss.	
* <u>Soymida febrifuga</u> A.Juss	"ROHANI"
<u>Swietenia febrifug</u> Willd.	
* <u>Cedrela toona</u> Roxb.	"TOON"
<u>Chloroxylon swietenia</u> D.C.	"BHIRRA"
<u>Swietenia chloroxylon</u> Roxb.	
RUTACEAE	
<u>Aegle marmelos</u> Correa	"BEL"
COMBRETACEAE	
* <u>Terminalia balerica</u> Roxb.	"BAHERA"
<u>Terminalia arjuna</u> Bedd.	"KAHU"
<u>T.berryi</u> W.&A.	
<u>T.glabra</u> W.&A.	
* <u>Terminalia chebula</u> Retz.	"HARRA"
* <u>Terminalia tomentosa</u> W.& Arn.	"SAJA"
<u>T.alata</u> Heyne ex Roth.	
<u>T.crenulata</u> W.&A.	
<u>T.coriacea</u> W.&A.	
* <u>Anogeissus latifolia</u> Wall.	"DHOARA"
<u>Conocarpus latifolia</u> Roxb.	
CELASTRACEAE	
* <u>Eleodendron glaucum</u> Pers.	
<u>E.roxburghii</u> Wight	
EUPHORBIACEAE	
* <u>Bridelia retusa</u> Spreng	"KASAI"
<u>B.crenulata</u> Roxb.	
<u>B.spinosa</u> Willd.	
<u>B.squamosa</u> Gehr.	
* <u>Emblica officinalis</u> Gaertn.	"AONLA"

Phyllanthus emblica L.		
* Glochidion velutinum Wight		"KHONDA"
* Mallotus philippensis Muell.		"SENDUR"
Rottlera tinctoria Roxb.		
RHAMNACEAE		
* Zizyphus jujuba Lam.		"GERRIA","BER"
* Zizyphus xylopyra Willd.		"GHONTIA"
Z.elliptica Roxb.		
Z.coracutta Roxb.		
* Zizyphus rugosa Lamk.	(C)	"CHURNI"
Z.latifolia Roxb.		
* Ziziyphus nummularia W.&A.		
Z.microphylla Roxb.		
* Ventilago calyculata Tulsane	(C)	"KEOTI"
V.madraspatana Gaertn.		
SAPINDACEAE		
* Schleichera oleosa		"KOSUM"
S.trijuga Willd.		
BURSERACEAE		
* Garuga pinnata Roxb.		"GHARRI"
Boswellia serrata Roxb.		"SALAI"
B.glabra Roxb.		
B.thurifera Colebrooke		
ARALIACEAE		
* Heptapleurum venulosum Seem	(C)	"DEOSEMAR"
APOCYNACEAE		
* Holarrhena antidysenterica Wall		"DUDHI"
H.pubescens Wall.		
H.codaga G.Don.		
Echites antidysenterica Roxb.		
* Carrissa spinarum A.D.C.		"KORONDA"
* Ichnocarpus frutescens Br.	(C)	"DUDHI"
Echites frutescens Roxb.		
EHRETIACEAE		
* Cordia myxa L.		"CHOTA LUSARI"
* Cordia latifolia Roxb.		"LUSARI"
Cordia obliqua Willd.		
* Cordia macleodii H.f.&Th.		"DHAMIN"
Hemigymnia macleodii		
* Ehretia laevis Roxb.		"DITARANGI"
VERBENACEAE		
* Tectona grandis L.f.		"SURGWAN"
BIGNONIACEAE		
* Stereospermum suaveolens D.C.		"PANDRI"
Bignonia suaveolens		
* Stereospermum xylocarpum Benth.		"PANDRI"
Bignonia xylocarpa Roxb.		
Spathodea xylocarpa T.Anderson		
Oroxylon indicum Vent		"SUMPARAL"

RUBIACEAE

* Adina cordifolia Hook.f.		"HALDU"
Nauclea cordifolia Roxb.		
* Mitragyna parviflora (Roxb.)Korth		"MUNDRI"
Stephegyne parviflora Korth		
Nauclea parviflora Roxb.		
* Gardenia latifolia Aiton		"PHIPHAR"
* Randia uliginosa D.C.		"KATUL"
Gardenia uliginosa Roxb.		
* Randia dumentorum Lam.		"MENHAR"
Gardenia dumentorum Roxb.		

LILIACEAE

* Smilax zeylanica L.	(C)	"RAMDANTON"
S.marcophylla Roxb.		

PART 2

The following additional tree and climber species were recorded from Kanha Tiger Reserve by Maheshwari (1963), Schaller (1967), Panwar (n.d.) and Kotwal (n.d.).

Dillenia indica L.	
Dillenia aurea Sm.	
Miliusa velutina H.f.&Thoms.	
Eriolaena hookeriana W.& A.	
Grewia subinequalis D.C.	
Grewia abutifolia Juss.	
Balanites roxburghii Planch.	
Celastrus paniculata Willd.	(C)
Zizyphus oenoplia Mill.	(C)
Vitis repanda W.& A.	(C)
Moringa oleifera Lam.	
Indigofera arborea Roxb.	
Acacia catechu Willd.	
Combretum flagrocarpum Herb.Calc.	(C)
Hymenodictylon excelsum Wall.	
Wendlandia exserta D.C.	
Gardenia lucida Roxb.	
Gardenia gummifera L.f.	
Gardenia turgida Roxb.	
Nyctanthes arbor-tristis L.	
Schrebera swietenioides Roxb.	
Cryptolepis buchanani Roem.&Sch.	(C)
Stereospermum chelonoides D.C.	
Gmelina arborea Roxb.	
Antidesma diandrum Roth.	
Trema orientalis Bl.	
Ficus glaberrima Bl.	
Asparagus racemosus Willd.	(C)

APPENDIX II :TREE PHENOLOGY SAMPLE.

The following species of tree and climber were monitored from February 1981 until March 1982 inclusive with 4 specimens of each species recorded each month:

Shorea robusta	Cassia fistula	Terminalia balerica
Sterulia urens	Bauhinia racemosa	Terminalia chebula
Bombax ceiba	Bauhinia malabarica	Terminalia tomentosa
Ficus religiosa	Bauhinia retusa	Bridelia retusa
Ficus arnottiana	Ougenia dalbergiodes	Emblica officinalis
Ficus infectoria	Butea monosperma	Mallotus phillipensis
Ficus tomentosa	Dalbergia paniculata	Zizyphus jujuba
Casearia tomentosa	Pterocarpus marsupium	Zizyphus xylopyra
Madhuca indica	Lagerstroemia parviflora	Schleichera oleosa
Diospyros melanoxylon	Syzygium cumini	Buchanania lanzan
Albizzia odoratissima	Careya arborea	Lannea coramandelica
Semecarpus anacardium	Ehretia laevis	Tectona grandis
Stereopermum saeveolens	Stereospemum xylocarpum	Gardenia latifolia
Bauhinia vahlii	Ventilago calyculata	

The following species were monitored as indicated:

Saccopetalum tomentosum	:7 specimens from February 1981–March 1982.
Litsea polyantha	:4 " " July 1981–March 1982.
Litsea sebifera	:4 " " February 1981–March 1982 one dying specimen replaced by nearest conspecific in August 1981.
Grewia tilaefolia	:4 specimens from February 1981–March 1982 dead specimens replaced by nearest conspecifics in July and August 1981.
Ficus cunia	:1 specimen from February 1981–March 1982.
Ficus glomerata	:1 " " " " " "
Flacourtia ramontchi	:2 " " " " " "
Casearia graveolens	:2 " " July 1981–March 1982,1 tree in August 1981.
Embelia robusta	:1 specimen July & August 1981,2 trees from September 1981–March 1982.
Erythrina suberosa	:1 specimen from December 1981–March 1982.
Anogeissus latifolia	:4 specimens from February 1981–March 1982,3 specimens in May 1981.
Glochidion velutinum	:3 specimens in February & March 1981,4 specimens from April 1981–March 1982.
Garuga pinnata	:1 specimen from July 1981–March 1982.
Cordia myxa	:1 " " February–June 1981,4 from July 1981 until March 1982.
Cordia latifolia	:3 specimens from July 1981–March 1982,4 from July 1981 until March 1982.
Cordia macleodii	:2 specimens from February 1981–March 1982.
Adina cordifolia	:3 " " " " " "
Mitragyna parviflora	:1 " " " " " "
Herbarium specimen 256	:1 " " August 1981–March 1982.

The following tree species were omitted from the phenology sample owing to my failure to discover them as distinct species until early 1982 :

Holarrhena integrifolia   Kydia calycina   Randia dumentorum

APPENDIX III : Draft of a paper which summarizes part of Chapter 6.

Infanticide in an undisturbed forest population of Hanuman langurs, *Presbytis entellus*.

Explanations for the occurrence of infanticide in wild populations of Hanuman langurs (*Presbytis entellus* Dufresne;Colobinae) have aroused considerable controversy [1,2,3,4,5]. Such killing has been observed or inferred at three sites in India [1,6,7,8,9], executed by an invading male after supplanting the previous resident male from a bisexual troop. Two main hypotheses have been proposed to explain this phenomenon. The social pathology hypothesis [1,3,4,5] proposes that infanticide is an aberrant, maladaptive behaviour manifested in langurs living at abnormally high density under excessive, pernicious human influence. The sexual selection hypothesis [1,10], proposes that infanticide is an adaptive strategy in which the invading male curtails lactational amenorrhorea in newly acquired females, permitting quick breeding. Hence, the male during its brief troop tenure increases its reproductive success. Here, I report observations of langur infanticide from undisturbed forest in the Central Indian Highlands [11] which whilst consistent with the sexual selection hypothesis suggest that the social pathology hypothesis is untenable.

The Hanuman langur is a eurytopic, largely folivorous, semi-arboreal colobine widespread in south Asia. Individuals are commonly organised into unimale or multimale matrilineal troops of 20-30 animals and smaller all-male bands [1,11]. Infanticide,associated with rapid male replacement or 'takeover' in which band males invade unimale troops, has been observed at Jodhpur [8] and strong circumstantial evidence suggests its occurence at Dharwar [6,7] and Abu [1]. These sites generally have high langur and human density in degraded habitats with few predators [1,4]. In contrast, gradual male replacement in multimale troops or infrequent social change, without takeovers, has been observed in habitats ranging from remote undisturbed forest to farmland [1,2,4]. Noting the association between habitat and pattern of social change the social pathology hypothesis, of Dolhinow and Curtin, suggests that the unimale plus takeover organisation is abnormal. With a breakdown in normal social relations, the vulnerable infants are incidentally killed during escalated aggression among mature animals. Infanticide is not adaptive but results from an inability of langurs to endure habitats very different from those in which the species evolved [3,4].

The alternative hypothesis, mainly due to Hrdy, proposes that infanticide evolved as a result of intense, post-fertilization, intermale competition for reproductive access [1,10]. A male, if it achieves troop residency may have only 2-5 years, before being replaced by an invader. Reproductive success will, under most conditions [12], be increased if breeding is accelerated by killing un-weaned, un-related offspring, which are delaying females' subsequent ovulation. An infanticidal male may gain additional advantage, over a non-infanticidal animal, by reducing the reproductive success of the dead infants' father and by eliminating future potential competitors of its own offspring [12]. A female may be in a 'cruel bind' by favouring mating with infanticidal males as, if the trait is heritable, she would then produce successful infanticidal sons [1].

The evidence for and against each hypothesis is equivocal [2,3,4,5]. Although attempted falsification of the sexual selection hypothesis in the wild is not practical [13], the social pathology hypothesis can be refuted if takeover associated infanticide is shown to occur in a low or moderate density langur population residing in an undisturbed habitat [4,14].

Hanuman langurs were studied (1980-83) in Kanha Tiger Reserve, a 1945 km^2 tract of moist deciduous (sal) and dry deciduous (mixed) forest in the Maikal Hills of Mandla district in the central Indian state of Madhya Pradesh [11,15]. The intensive study area, the central Kanha maidan (22^o 17' N 80^o 38' E), is a mosaic of sal (*Shorea robusta*) forest and meadow. Human influence has been largely restricted to forestry operations some eighty years ago and slash and burn cultivation by Baiga tribal people probably creating the meadows in antiquity [11]. The reserve holds a diverse and high density large mammal population including many large predators [11,15]. Langur density on the Kanha maidan was 46.15 $/km^2$, troop density 1.79/km^2, band density 0.51/km^2, mean troop size 21.7 (range 11-34), mean band size 14.0 (8-18), population adult sex ratio 1:2.5 and troop adult sex ratio 1:7.9 (1:1.3-12). Of 14 troops 13 were unimale and one trimale. The birth season was December until May, with a median in February.

A well habituated unimale troop "C" which ranged over 74.5 ha, was watched for some 2000 hours between February 1981 and March 1982. It consisted of an adult male with 9-13 adult females, 3-4 subadult females and up to 12 other immatures. During April and May 1981 a social change occurred, summarized in FIG 6.21, in which a 13-16 member band "Q" attacked "C" and during four days (Phase 1) killed three infants (1 male, 1 female, 1 unknown sex) out of six (< 2-3 months old) present. The actual infanticide by "Q" males was observed on the first two occasions whilst the third death was missed by some 30 s as "Q" males chased the infant-bearing female out of view. On regaining contact, the female was sitting amongst "Q" males with a dead, bitten infant in its lap; it was concluded that infanticide by "Q" occurred. Attacks were highly directed, with only infant bearing females being attacked and only infants injured. Two infants died immediately and one after two hours with extensive bite wounds to head, thorax and abdomen. Two langurs were abandoned at death whilst one was carried by the female for three hours. A recently immigrated six month old infant female was attacked twice whilst on its presumed mother and later noted with injuries. Each attack was made by a sub-group of 3-5 large males, but the precise identities of the infanticidal animals are unknown; the largest "Q" male, AM24, was involved but the whereabouts during the assaults of AM30, AM23's successor, is unknown. The "C" resident 'AM23' was ineffectual and only successfully countered one out of five "Q" attacks; it was not present in the vicinity of the infanticides. "C" tended to breakup on the approach of "Q" with infant bearing females fleeing into apparent concealment, including sub-terranean streams, whilst unencumbered females associated with the band. The dead infant's mother is unknown in one case and identities are probably known in two cases. The sire of the killed infants is unkown but is much more likely to have been the resident ('AM23') than any "Q" male.

In Phase 2 (FIG 6.21) "C" frequently formed sub-groups, rejoining at night, with 'AM23' and infant-bearing females remaining separate (100-500m) from "Q" whilst the remaining females consorted with the band. Two adult females mated with AM24 and solicitations, rarely observed in the month prior to band invasion, were common. The band attacked the infant-bearing sub-group once during this period and one female carrying an infant eluded pursuing males. With the replacement of 'AM23' by a "Q" male 'AM30' (Phase 3, FIG 6.21), polarization ended and frequent attacks by 'AM30' on infant-bearing females began, which subsided in June. In late May, when attacks were diminished, the frequency of violent adult male-female interactions during 12 days of dawn to dusk observations was 2.83/day ± s.d. 2.12. Females intervened in 68 % of 31 such attacks for which there are data. The frequency of occurrence of these male assaults on 138 complete days, spread equally across the year, was 0.61/day ± s.d. 1.16. The circumstances of the male replacement were not observed, AM23 was last seen with "C" on the morning of 5 May but by the afternoon it had disappeared and AM30 (without "Q") was troop male. AM23 was never seen again. During the period of takeover the six month old infant was attacked but despite serious wounds survived; no infant disappeared. From mid-May "C" troop had occas ional agonistic encounters with band "Q" and no consorting with "C" females occured. In the subsequent birth season ten infants were born which, assuming a 200 day gestation [1], suggests that first conceptions occurred in late May. This indicates that 'AM30' was most likely the sire. Between August and October two infants, born pre-takeover, disappeared in unknown circumstances and 'AM30' remained "C" resident at least until May 1983.

The above observations of infanticide in undisturbed forest with moderate langur density (species range 2-133/km^2) is strong evidence that the social pathology hypothesis cannot be supported, at least in Kanha. The restriction of injurious aggression by band males to infants, infant-bearing female concealment and sub-group formation suggest a predictable pattern with infants as targets of band attacks. Birth intervals for two females in which the infant survived to weaning were 24 and 29 months. The mean birth interval for five infant deprived females was 11.7 ± s.d. 1.61 months (2 being probable mothers of infanticide victims and 3 the mothers of infants which disappeared in unknown circumstances). Therefore the essential components of the sexual selection hypothesis, that the invader should not kill its own offspring but should sire and accelerate post-takeover conceptions are not violated by the Kanha observations. The latter two conditions are directly confirmed.

Infanticide has usually been reported as occurring after takeover but the reversed pattern observed here has approximate precedents [1]. Pre-takeover infanticide may erode the advantage to the resident of staying as troop male and hence perhaps accelerate takeover and increase the probability of a successful band invasion. Faced with an infanticidal band the resident's best strategy may be to desert, thus terminating investment and trying again elsewhere. The strategy may depend on such probabilities as the resident being injured, of defeating the band, of being the infant's father and of future reproductive success as a troop or band male elsewhere. It is not known if AM30 was infanticidal, but if such a male or kin takeover, the pattern is consistent with the sexual selection hypothesis.

If takeovers are part of an extra-troop male strategy to increase reproductive success it is predicted that the optimal time for invading troops would be between birth and mating seasons. If invasion was to occur after the mating season the receptive females would probably have already been inseminated. New residents do not kill post-takeover births [1]. Therefore, takeover before the birth season would result in a cohort of infants appearing at the onset of the males tenancy, obstructing his reproductive access. The temporal distribution of takeover onset from the literature [1,6,8,9] and Kanha, relative to the birth season peak [16,17,11], is shown in Fig.6.23. The data agree with the predicted timing of takeover and provide strong circumstantial evidence for infanticide being an adaptive male strategy.

However, why has infanticide been seen at some sites and not others ? One possibility is that the frequency of takeover-associated infanticide is related to particular demography [18], perhaps with infanticidal behaviour occurring as a mixed Evolutionarily Stable Strategy [12]. It has been suggested that infanticide is associated with high population density and a predominantly unimale structure [1,2,18], which by producing a high proportion of 'dissatisfied' band males may result in a high frequency of takeovers. An association between infanticide and unimale structure is supported by the intra-specific variation shown in Fig. 6.9. But, because the functional reasons for the evolution of unimale-multimale patterns are not understood [19], it is not yet possible to disentangle cause and effect. However, the data suggest that troop composititition, and not density may predict the distribution of infanticide among langur populations.

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APPENDIX IV : SUMMARY OF DAILY FIELD NOTES 18 APRIL - 16 MAY 1981. SOCIAL CHANGE AND INFANTICIDE : "C" TROOP AND "Q" BAND.

In this appendix, summarized daily field notes are presented for the period of social change and infanticide in "C" troop, Kulloo chattan study area, Kanha meadows. The time the observer spent with "C" troop is given in parentheses after the date (for abbreviations see Table 4.A;

All behavioural terms follow Dolhinow (1978). xx' indicates an animal, were identity not known, but is recognisable within a days observation.

18 April 1981 (dawn to dusk follow).

09.55 "Q", an all-male band of 13 males,observed for the first time suddenly initiated an encounter with "C" at Kuloo chattan. "C" flee and within a melee of chasing a AMQ pursued an AFIN1 and snatched the infant from the female's chest. The AMQ held the infant (IN117,female,'pinkface',two weeks old) and repeatedly bit it, leaving it lying injured in the leaf litter before moving away. Another AMQ walked to IN117, touched it with its hand, grimaced and walked away.

10.10 "C" arboreal, "Q" terrestial. An AF' retrieved IN117 and ascended with it into a tree.

10.20 Eight "Q" males ended encounter lull, ascended trees and chased AF'IN117 through canopy. AF' flees squealing holding injured infant to chest with a forearm. During a bout of chasing between "C" females and "Q" males a AMQ grapples with AF' and IN117 falls 20 m to the forest floor. Immediately chasing and vocalisations cease, "Q" langurs descend.

10.25 AM23 resighted on troop periphery by observer. Six "Q" adult males chase it to the east and out of sight. Meanwhile a AMQ walks to IN117 lying alone in the litter, picks it up with both hands and whilst sitting,bites it three times in the trunk. At the third bite a sub-adult female 10 m distant squeals,descends, runs towards the male. The male looks up, drops IN117 and runs away. The sub-adult female retrieves infant,which is breathing rapidly and deeply with eyes closed,and manually inspects it.

10.35 The sub-adult female abandons the infant on the forest floor and ascends a tree. Binocular examination of the infant shows it to be still breathing but with intestines protruding from abdomen and probable lung tissue from the chest.

10.50 AM23 re-appears, teeth-grinding, and faces "Q". "C" largely arboreal and quiet, hard to locate.

11.19 SF' and AF' descend to IN117. SF' retrieves infant and manually inspects it before transferring it to AF'. AF' visually inspects infant but when she begins to walk away, infant falls off her chest. AF' moves 0.5 m from it and feeds. AF' is probably the same langur as was carrying infant during 10.20 arboreal chase and was probably AF28.

11.20 "Q" terminate encounter with "C" after a series of "Q"- AM23 chases.

12.05 SF', AF', still in close proximity to IN117, embrace and squeal. SF' departs vicinity.

12.30 AF' rejoins "C", abandoning IN117 on forest floor. The infant died at about this time.

13.53 AF' returns to carcase, looks at it from 0.5 m away and ascends into canopy. Return to "C" not recorded, but prior to 16.00 hours.

19 April 1981 (dawn to dusk follow).

05.50 Located "C", to find that AF22 and IN225 had immigrated from "B". "C" in encounter with "Q" males, who were seen to chase AF22IN225 through canopy. A lull in encounter until 07.35.

07.35 Five large adult males of "Q" suddenly appear chasing AFIN1 of "C" across 150 m of open grassland. AFIN1 halts in open meadow and faces males, one of whom is AM24. A large male grapples with AF and takes infant (IN118, male, 'brown face', 6-8 weeks old). Whilst sitting,the male holds infant with both hands and repeatedly bites into it's trunk. During killing AF' moves some 60 m away and as the male drops infant to the ground the female runs to a stream bed. A second adult male picks infant up and bites into it, but it appeared to have died at the first attack.The five males sat for a few minutes scattered about the corpse, grunting and gazing about before departing. AM23 appears 'teeth-grinding' from the forest and faces "Q". AM23 runs towards "Q", displays and whoops.

08.45 "Q" adult males chase AF22IN225 but are eluded.

08.50 The 13 males of "Q" terminate encounter and "C" langurs appear from a scatter of locations and aggregate as a troop.

20 April 1981 (dawn to dusk follow).

An encounter between the sixteen member "Q" and "C" from 08.00 to 09.40 hours. Onset was heralded by AM23 alert behaviour, grunting and a foray towards the approaching band. AM23, SF and AF remain whilst AFIN1 and some AF flee 200 m to a tree lined stream where I find them very hard to locate. As "Q" initiates encounter two SFc run squealing to the males and "Q" chases AM23. Five large "Q" males progress to stream, do not appear to notice any infant bearing females and on coming into contact with "B" troop retreat 200m. At 08.49 an infant bearing female moves by the stream, "Q" males alert, grunt, AM23 advances teeth grinding but is chased back by a "Q" male. At 08.54 adult males of "B" (AM6 + 2 others) run towards the AM23 - "Q" encounter. Simultaneously AM23 and the three "B" males advance towards "Q" which descend en mass and move away. At 09.02 "B" males depart. The combination of "B" and "C" males resulted in the supplantation of "Q" and its displacement from proximity to the infants. AM23 when acting alone failed to achieve this. "Q" finally terminated encounter at 09.30. "Q" identified by presence of AM24, 26 and SM27 marker individuals.

Therefore during this "C"-"Q" encounter "Q" males did not come into close proximity to AFIN1's as a result of "C" polarization, concealment and action of "B" males during "C"-"Q" encounter.

21 April 1981 (dawn to dusk follow).

09.45 AF11 of "B" transfered to "C" resulting in "B" becoming the all-male band "R".

09.50 Adult females grunt, watch bipedally as "Q" approaches. "Q" initiates encounter with "C", two sub-adult females run towards "Q". Most of remainder of "C" flee across meadow pursued by four "Q" adult males. Two AMQ chase AF22IN2, males attacks twice but IN2 remains on females chest. AF22 twice presents (without head shake) towards AMQ with IN2 clinging ventrally. AM23 chases males from vicinity of AF22.

10.00 A number of AFIN1 are apparently concealed in tall grassland. One of them moves a short distance. Several adult males alert and leap forwards into the air ('stotting'), peering into the grassland. Males then ascended into adjacent trees and peered into the grassland. One adult female with infant was observed hidden in a sub-terranean nullah.

10.15 Suddenly a AF'IN1 is sighted being pursued from the patch of long grass, some 250 m across open meadow, by four "Q" males. On regaining contact (lost visual contact for 60 s) AF' was sitting with a dead infant in its lap (IN119, unknown sex,6-8 weeks old,grey face). The four AMQ were sitting in an arc 10 m from AF' grunting and looking around. Neither the actual injurious actions or the identities of the attackers were recorded.AF' probably AF29

10.28 An AMQ chases AF'IN1(dead) a short distance, AF' squeals and runs away from "Q" and "C",carrying infant.

10.40 The chase terminating in infant death brings "Q" into an encounter with AMA until 11.15

11.30 AF' sits with dead infant in lap 100 m from "C". Ventral surface of female covered in blood. IN119 ventral abdomen ripped open;it probably died instantly. AMA supplants "Q"; band moves into "C" range.

12.55 "Q" terminates encounter with "C".

13.00 AF' carries infant carcase to 50 m from "C", four times leaving it and then retrieving it as Jungle Crows (C.splendens) descend to feed on the infant.

13.40 AF' abandons carcase and crows and Tree Pies (D. vagobunda) scavenge the infant. AF' rejoins "C".

14.35 AF' being trailed, by three sub-adult females who follow it at 1-3 m distance. The sub-adults lay hands on the blood coated AF', embrace and mount. They gaze into AF' face from less than 0.5 m distant which grimaces. This 'shadowing' behaviour (lasting 1 hour) was only seen on this occassion. IN225 found to have a cut at tail base, perhaps inflicted during chase by "Q" at 09.50 hrs.

22 April 1981 (dawn to dusk follow).
"Q" not observed.

23 April 1981 (06.30-08.00)
Three adult females and four sub-adult females of "C" consorting with band "Q", out of sight of main body of "C".

25 April 1981 (17.00-18.50)
"Q" not observed.

26 April 1981 (dawn to dusk follow).
"Q" not observed.

27 April 1981 (dawn to dusk follow).
Encounter between AM23 and "Q" (mainly AM24) from 11.40 to 14.40 with whoops, displays, chases and counter-chases. The three AFIN1 remain inactive and in concealment throughout. AMQ do not come into proximity to infants. "C" females do not consort with band.

28 April 1981 (dawn to dusk follow).
"Q" not observed.

29 April 1981 (dawn to dusk follow).
"Q" not observed.

30 April 1981 (dawn to dusk follow).

10.50 On the approach of "Q", "C" polarizes with AFIN1's and AM23 fleeing 200 m whilst a group of sub-adult and adult females without infants remain in path of "Q"'s approach.

10.55 AM24 and two other adult males of "Q" chase after AFIN1 component of "C",watch into a patch of long grass where the infant-bearing females went to ground. Suddenly the "Q" males jump into the grassland, AFIN1 runs out and goes down in another patch of long grass 50 m distant. Adult males chase, 'stott' and and watch into the patch.

11.12 The non-infant bearing females in proximity to remaining 13 members of "Q". AF11, 15 m from a AMQ head shakes (without present).

11.13 AF11 walks to two AMQ, presents with head shake repeatedly. AM's watch, grunt and grimace.

11.20- 12.10 AM23 supplants the three "Q" males from close proximity to infant-bearing females.

13.20 Polarization increased with AFIN1 and AM23 in the south-west of the grid,some 450 m from the rest of "C". Three adult females including AF29,11 and four sub-adult females consort with "Q". AF29 presents (without head shake) 1.5 m from AM24. AM24 mounts AF29 three times with probable intromission and ejaculation. Three "C" sub-adult females sit 2 m from the couple and do not harass the mating AM23, occasionally whooping and displaying, watches across half a kilometre of open meadow towards "Q".

15.15 "Q" and consorting females progress away from and out of sight of AM23, feed.

16.25 AM23 leads progression of infant-bearing females from towards consorting females and "Q".

17.50 "Q" seperates from "C" consorts by progressing to the north.

18.15 AM23 rejoins "C" consorters and sleeps with them some 150 m from the infant-bearing component of "C".

2 May 1981 (08.00-10.00)

Eleven "C" langurs (6 AF, 4 SF, 1 IN2) consorting with "Q" Rest of "C" containing infants and AM23 some 400 m to the south west. An adult female presents and head shakes to AMQ.

3 May 1981 (06.00-09.00)

Similar polarization to 2 May; females without infants consorting with "Q". Infant-bearing females and AM23 200 m away. AM23 watching frequently towards "Q" and grunting occasionally.

4 May 1981 (06.00-09 00, 17.00-19.00)

06.30 Three adult females and four sub-adult females progress 200m from "C" to "Q".

06.35 A sub-adult female presents and head shakes to an AMQ.

07.20 Brief agonism between "Q" and AM23, chase, display, whoops.

08.05 IN225 and two adult females among consorters, present and head shake to AMQ.

17.40 Consorting sub-group of "C" with "Q". AF11 presents and head shakes to an AMQ, which mounts AF11 twice, ejaculation possible. AM24,26, SM27 present in "Q".

17.55 An adult female and sub-adult female head shake and present to a AMQ.

18.03 Consorting sub-group and "Q" seperate.

18.10 IN225 found to have a chest wound at or about the location of the left nipple and an injured left wrist. Perhaps injury from a fall, predator attack or "Q" male attack. Infant inactive, crouched among roacks.

18.40 The consorting sub-group sleeps between "Q" and infant-bearing sub-group., 150 m from "Q" and 100 m from rest of "C".

5 May 1981 (05.30-09.30, 18.00-19.00)

05.45 "C" divided at sleeping site into two subgroups, consorters (6 AF,4SF including AF29,28) approach "Q"; infant-bearing females and AM23 remain seperate from "Q".

06.25 AF22 presents, with head shake, three times to a AMQ.
06.41 AM23 observed for the last time.
06.45 A sub-adult female presents, with head shake, to a AMQ.
07.47 Two subadults and adult female present to AM' of "Q". The rest of "Q" (15 males) moved from vicinty at 07.55. AM' remains.
08.26 During a bout of AFC grooming AM', AM' suddenly chases IN225 arboreally. AF22, SF chase AM',intervene and wrestle with it. After a few seconds all quiet and still. IN225 presents and head shakes towards AM' from 5 m away. An adult female presents and head shakes towards AM'.
08.32 AM' gradually moving towards IN2, suddenly IN225, AF, SF descend tree en masse. AF22IN225 chased on ground by AM' but AFC intervenes and chases AM' away.
09.15 AM' walks towards tree containing solitary IN225. AM' looks up towards infant and immediately AF, SF chase AM' for 50 m.
18.15 A melee among consorters and AM'. An infant-bearing female being chase by AM', which is chased by intervening females, arboreal. Frequent presents with head shakes directed by females towards AM'. AM' is not AM23 but AM30 from "Q".
18.30 AM30 sleeps with "C". "Q" sleeps some 100 m away.

7 May 1981 (07.00-09.00, 17.00-19.00)
"C" with AM30. "Q" within grid but not observed in proximity to "C".

10 May 1981 (17.00-18.30)
"Q" including AM24 moving interspered with "C". Little overt interaction between "C" and "Q".

11 May 1981 (17.00-18.30)
"Q" moving interspered among "C". Little overt interaction between "Q" and "C" observed.

13 May 1981 (18.00-18.30).
"C" moving alone. "Q" not observed.

14 May 1981 (dawn to dusk follow).
"C" unimale with AM30. Frequent interactions between AM30 and adult and sub-adult females. AM30 chases infant-bearing females with violent interventions by other females, frequently with explosive 'ha ha ha!' vocalization. AM30 often chased from close proximity to AFIN1s by females not bearing infants. AM30 rarely groomed by females. Solicitations of AM30 by females without infants frequent. AM30 occassionally 'teeth grinds' facing "C" females.

15 May 1981 (dawn to dusk follow)
Frequent AM30-female interactions, agonistic and solicitations. AM frequently chasing AFIN1s and consequently being chased by non-infant bearing females. AM30 not seen to make physical contact with any infant-bearing females.
14.55- 15.10 "Q"-"C" encounter with troops moving through each other with only one aggressive interaction, between AM30 and AMQ. No presenting by "C" females to "Q".
17.35- 18.40 "Q"-"C" encounter with AM24-AM30 chases, teeth-grinding, displays. "Q" terminates encounter and "C" wins.

16 May 1981 (dawn to dusk follow).
Frequent AM30-"C" female interactions as a result of AM coming into close proximity to infant-bearing females. Solicitations by "C" females to AM30 common.
06.49 -07 15 "Q"-"C" encounter, mainly between AM24, AM30, chases, teeth-grind.

APPENDIX V.A. LANGUR CENSUS :APRIL 1981.

KANHA MEADOW.

All troups within 7.8 Km^2 of Central Kanha meadows censused April 1981,except * censused 23 May 1981) [+ = multimale troop]

Troop	Type	Langur Sex/Age Category									
		AM	AF	SM	SF	J	JM	JF	IN2	IN1	TOTAL
"A"	Troop	1	11	5	3	5	1	4	1	8	34
"C"	Troop	1	12	0	3	2	0	2	0	8	26
"CH"	Troop	1	10	0	3	1	0	1	4	3	22
"DN"	Troop	1	12	0	1	9	2	1	1	4	28
"F"	Troop	1	11	3	1	3	2	1	4	4	27
"HC"	Troop	1	6	1	2	2	0	2	0	1	13
"KM"	Troop	1	8	0	5	2	2	0	0	4	21
"KO"	Troop	1	8	1	2	2	2	0	0	6	20
"M"	Troop	1	5	0	5	0	0	0	0	0	11
"MO"	Troop	1	11	0	1	0	0	0	0	9	22
"SH"	Troop	1	10	0	2	0	0	0	4	4	21
"ST"+	Troop	3	4	6	0	1	0	1	0	1	15
"N"*	Troop	1	9	1	1	8	-	-	2	1	23
"Z"	Troop	1	10	0	5	2	2	0	0	4	21
"1"	Band	9	0	9	0	0	0	0	0	0	18
"2"	Band	12	0	6	0	0	0	0	0	0	18
"3"	Band	6	0	6	0	0	0	0	0	0	12
"P"	Band	8	0	0	0	0	0	0	0	0	8
Total:all groups		51	127	38	34	37	11	12	16	57	360
Total:Troops		16	127	17	34	37	11	12	16	57	304
Total:Band		35	0	21	0	0	0	0	0	0	56

DEOTALAO

(Troups visiting waterhole at Deotalao, censused April 1981)

Troup	Type	AM	AF	S	SM	SF	J	IN2	IN1	TOTAL
1	Troop	1	13	3	-	1	3	0	6	26
2	Troop	1	10	7	-	3	1	0	7	26
3	Troop	1	6	0	0	0	5	0	0	12
4	Troop	1	13	3	-	-	2	1	7	27
5	Band	10	0	6	6	0	0	0	0	16
6	Band	11	0	7	7	0	0	0	0	18
Total:all groups		25	42	23	13	4	8	1	20	125
Total:Troops		4	42	10	-	4	8	1	20	91
Total:Bands		21	0	13	13	0	0	0	0	34

[For Langur sex/age class abbreviations and descriptions see Table 4.A]

APPENDIX V.B. SUMMARY OF "C" TROUP COMPOSITION CHANGES.

Composition January 1981:	May 1983
AM23,	AM30,
AF5,28,29,31,36,38,39,42,45,	AF5,11,22,28,29,31,36,38,39,42,45,49,50,
SF49,50,52,53,	SF53,25,35; JM55,59,73; JF54,56,60,61,
	IN2m74,75; IN1 76,77,78.

DATE 1981 change noted	Langur I.D.	Troop size after event	Nature of change
28-29/1	F35	15	Born to AF5.
7-12/2	*	16	Birth.
16-24/2	*	17	Birth.
25-26/2	*	18	Birth.
28/2-13/3	F47	19	Birth to AF36.
2-16/4	F17	20	Birth probably to AF28.
18/4	IN1f17	19	Death, infanticide by "Q"
	AF22	20	Immigration from "B" troop.
	IN2f25	21	Immigration from "B" troop.
	IN1m18	20	Death, infanticide by "Q"
21/4	AF11	21	Immigration from "B" troup.
	IN1x19	20	Death, infanticide by "Q"
5/5	AM23	19	Missing, presumed dead or emigrated.
	AM30	20	Immigration from "Q" troup.
26/6	IN1f46	--	Matured to IN2 status.
	IN1f35	--	Matured to IN2 status.
14/7	IN1f47	--	Matured to IN2 status.
30/7-11/8	IN2f47	19	Missing, presumed dead or emigrated.
16/8	IN2f25	--	Matured to JF status.
1-28/9	IN2f46	18	Missing, presumed dead or emigrated.
8-15/12	F54	19	Birth to AF11.
12-14/1	M55	20	Birth to AF38.
15-16/1	F56	21	Birth to AF28.
19-20/1	F58	22	Birth to AF39.
16/2	IN2f35	--	Matured to JF status.
24-26/2	SF49	--	Matured to AF status.
	M59	23	Birth to AF49.
3-15/3	F60	24	Birth to AF36.
19-20/3	F61	25	Birth to AF29.
12-14/4	M73	26	Birth to AF42.
29/4-21/5	SF50	--	Matured to AF status.
	M74	27	Birth to AF50.
21-27/5	M75	28	Birth to AF45.
	IN1f58	27	Missing, presumed dead or emigrated.
1983			
20/6/1982-	SF52	26	Missing, presumed dead or emigrated.
-9/4/1983	F76	27	Birth to AF5 (estimated January 1983)
	M77	28	Birth to AF39 (" " ")
	M78	29	Birth to AF22 (" " ")
	IN1f54	--	Matured to Juvenile status.
	IN1m55	--	Matured to Juvenile status.
	IN1f56	--	Matured to Juvenile status.
	IN1m59	--	Matured to Juvenile status.
	IN1f60	--	Matured to Juvenile status.
	IN1f61	--	Matured to Juvenile status.
	IN1m73	--	Matured to Juvenile status.
	IN1m74	--	Matured to IN2 status.
	IN1m75	--	Matured to IN2 status.

APPENDIX V.C. SUMMARY OF LANGUR RELATIONSHIPS WITHIN "C" TROUP.

Age/sex class and known relationships for all members of "C" troop January 1981 to May 1983 (Abbreviations-see Table 4.A).Possible paternity indicated as the adult male present in the troop during the estimated month of conception.

Adult Male : AM 23 AM 30

Adult Female	: AF 05	AF 11	AF 22	AF 28	AF 29	AF 31	AF 36
Offspring	F35 F76	F54	F25 M78	F17 F56	X19 F61		F47 F60
	* +	+	x +	* +	* +		+ +

Adult Female	AF 38	AF 39	AF 42	AF 45	AF 49	AF 50
Offspring	M55	F58 M77	F46 M73	M75	M59	M74
	+	+ +	+ +	+	+	+

Possible father: AM 6 = x ;AM23 = * :AM30 = +.

Subadult Female: SF 52 SF 53

APPENDIX V.D ADULT AND SUB-ADULT FEMALE HISTORIES.

In the following three pages the reproductive histories of "C" troop females are summarized. For abbreviations see Table 4.A. See also Chapter 6, Appendix V.B,C.

F = Female

M = Male

langur identity (provisional) - - - - -

langur identity (confirmed) ———

birth

Transfer of "B" animal to "C". ▼

Maturation △

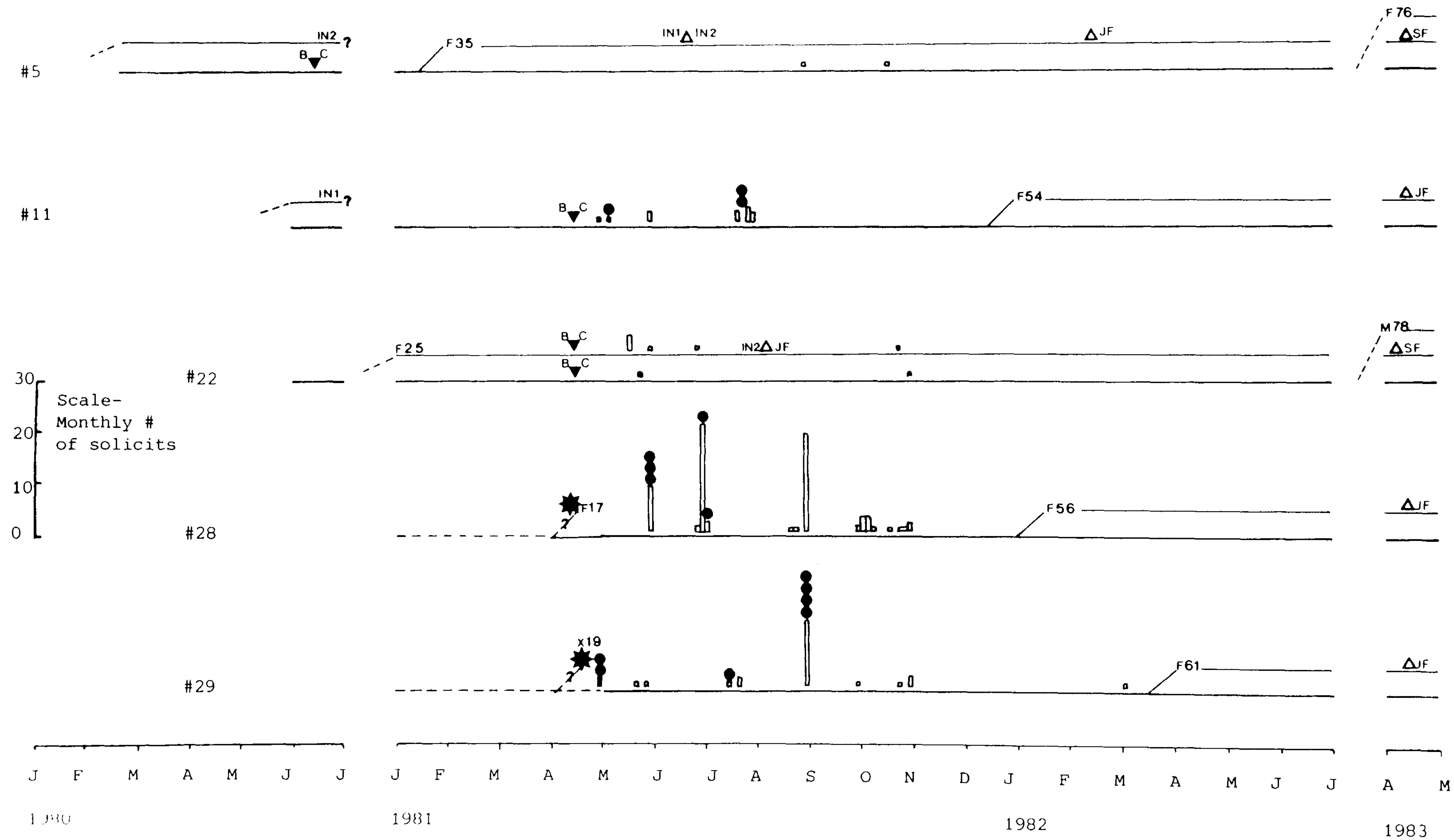
Infanticide ✸

Disappearance ★

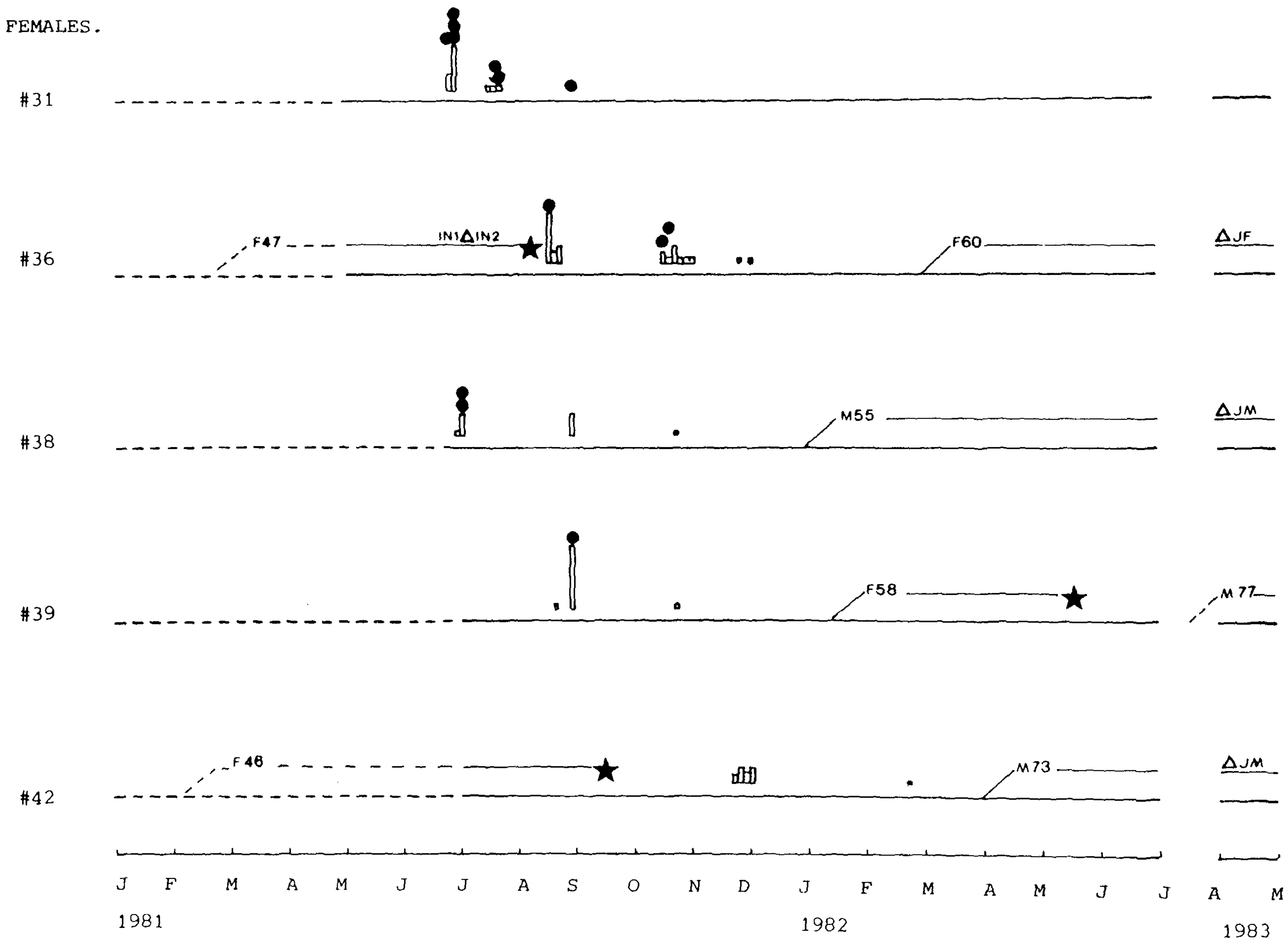
Copulations ●

(Copulations and solicitation frequency are expressed as the number of occurences opportunistically observed per day)

APPENDIX V.D : HISTORIES OF "C" FEMALES (see Chapter 6).

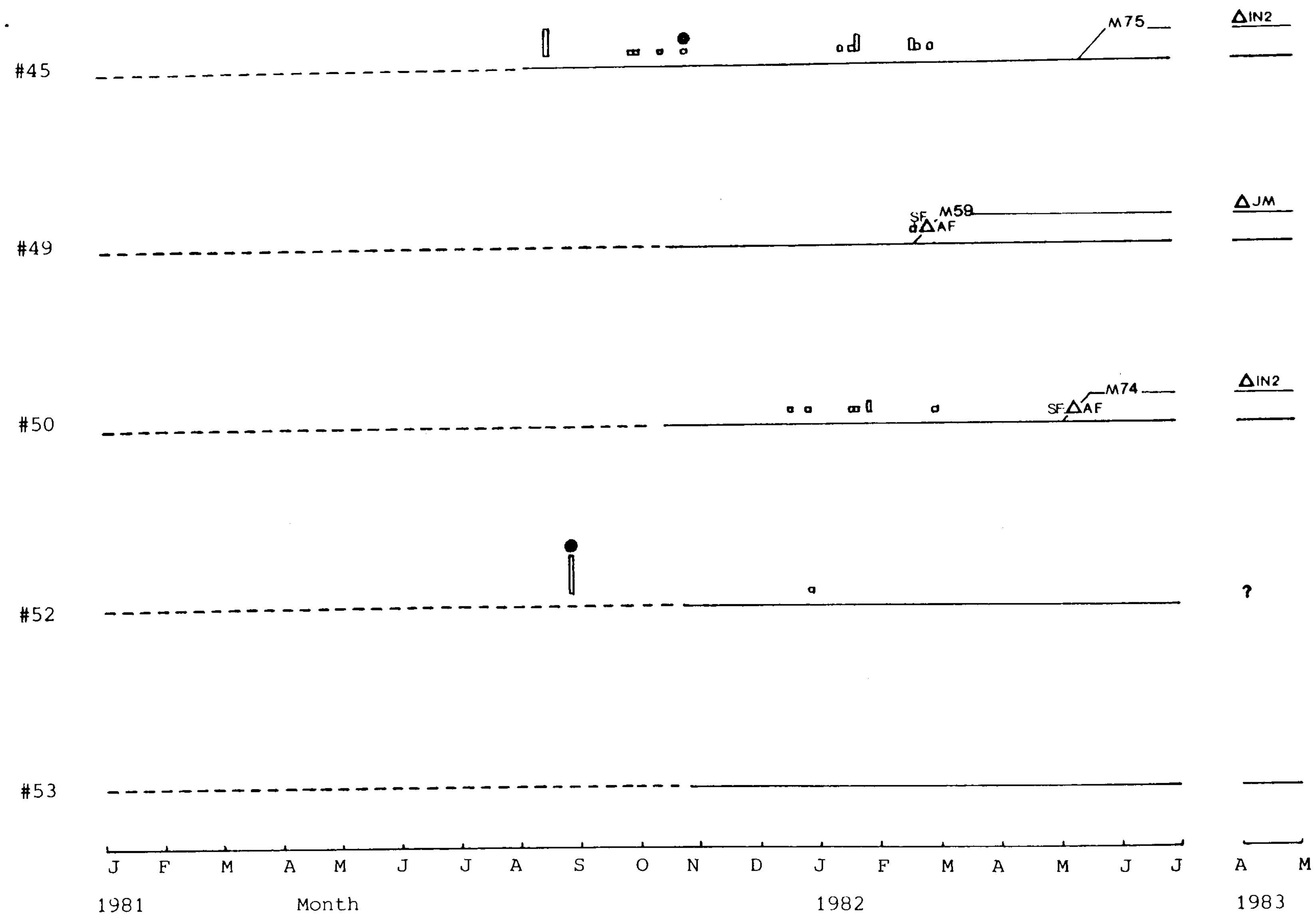


APPENDIX V.D (page 2):
HISTORIES OF "C" FEMALES.



APPENDIX V.D (page 3):

HISTORIES OF "C" FEMALES.



APPENDIX V.E : Species of herb and grass consumed by "C" troop.

Species	**Family**	**Plant part**
Cynoglossum wallichi	Boraginaceae	seed
Acanthospermum hispidum	Compositae	entire
Plectrocanthus icanus	Labiatae	seed
Tridax procumbens	Compositae	flower
Cassia tora	Leguminosae	leaf
Vitis latifolia	Vitacae	leaf
Flamengia bracteata	Leguminosae	seed
Scleria tessellata	Cyperaceae	seed
Oryza sativa	Graminae	seed

APPENDIX V.F PERCENTAGE RANGE OVERLAP BETWEEN MONTHS.
Sum of shared percentages, see Chapter 8.

MONTH	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR
APRIL	100.0	41.9	35.2	42.5	42.0	40.4	34.7	33.2	38.3	26.2	37.7	40.7
MAY		100.0	54.1	44.2	52.2	48.8	40.9	44.0	43.8	47.1	50.7	54.4
JUNE			100.0	51.7	44.9	45.2	39.9	40.2	38.2	48.2	48.3	50.3
JULY				100.0	55.2	56.2	43.7	41.8	50.2	51.0	52.1	48.1
AUGUST					100.0	56.3	38.9	42.8	49.0	41.5	49.9	55.5
SEPTEMBER						100.0	43.7	45.8	52.3	47.4	47.2	44.1
OCTOBER							100.0	45.8	46.7	39.0	41.0	49.4
NOVEMBER								100.0	55.6	37.3	36.0	37.4
DECEMBER									100.0	43.9	44.8	48.4
JANUARY										100.0	50.6	45.0
FEBRUARY											100.0	57.2
MARCH												100.0

APPENDIX V.G MONTHLY FEEDING BUDGETS : PERCENTAGE OVERLAP.
sum of shared percentages, see Chapter 9.

ITEMS

	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
April	100	38.5	39.8	39.6	28.6	33.1	26.9	27.7	11.7	33.2	48.7	60.2
May		100	87.8	56.7	38.7	28.7	71.1	25.4	13.1	15.0	22.4	16.0
June			100	51.5	36.2	25.2	69.6	26.6	12.9	16.0	23.2	16.6
July				100	57.0	44.1	46.5	40.7	25.7	27.6	36.1	20.3
August					100	78.1	57.0	65.5	56.2	57.2	56.9	15.0
September						100	50.1	73.9	64.1	66.3	64.0	24.4
October							100	44.4	32.3	32.0	40.2	11.4
November								100	81.3	70.5	57.7	17.8
December									100	66.7	45.2	12.9
January										100	67.8	33.9
February											100	55.9

SPECIES AND ITEMS

	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
April	100	20.2	13.5	14.2	4.9	5.6	2.9	3.4	3.0	3.4	8.0	11.8
May		100	52.9	20.6	4.9	5.3	3.1	3.1	4.2	4.5	5.8	6.5
June			100	18.2	4.7	4.3	1.5	1.4	0.1	2.0	3.4	3.3
July				100	17.6	19.6	10.9	12.3	12.8	11.1	10.0	4.5
August					100	39.7	13.8	18.9	25.3	20.4	14.6	3.8
September						100	35.7	44.9	46.1	36.3	23.7	4.8
October							100	27.0	24.0	21.3	13.3	3.0
November								100	75.6	60.6	36.6	4.0
December									100	55.8	32.3	4.3
January										100	40.2	10.8
February											100	23.8

APPENDIX V.H. Phenology availability index and climate data. See Chapters 3,4 & 9.

Month	Availabilty Index							Climate data	
	1	2	3	4	5	6	7	8	9
April	204.72	199.93	101.57	45.27	40.69	213.00	169.07	0	37.8
May	261.20	236.55	74.17	54.08	21.56	179.30	284.68	8	39.4
June	311.61	139.45	93.87	205.39	2.25	2.82	109.45	329	36.7
July	381.61	47.92	56.64	133.94	4.89	2.85	63.32	525	28.1
Aug	394.82	28.04	22.66	34.58	1.12	3.32	32.37	133	29.0
Sept	395.58	5.55	4.30	32.05	2.69	0.02	28.31	208	31.2
Oct	393.23	3.68	4.69	2.79	1.39	0.45	19.13	0	29.8
Nov	394.85	32.07	33.11	31.55	2.04	0.90	18.35	0	27.1
Dec	394.08	46.25	46.90	46.38	0.77	0	19.99	25	24.8
Jan	377.84	32.1	51.03	51.04	3.12	0.12	18.02	20	25.6
Feb	322.36	38.32	136.12	136.37	80.29	0.70	15.71	3	25.6
March	202.72	207.98	140.01	109.99	262.63	80.28	10.52	8	31.4

1-9 Availability index for each phytophase.

1 Mature leaf
2 Young leaf
3 Open leaf bud
4 Leaf bud
5 Flowerbud
6 Flower
7 Fruit
8 Total monthly rainfall/mm
9 Mean maximum daily temperature per month/^{o}C