SPACE-USE PATTERNS OF THE INDIAN GIANT SQUIRREL (Ratufa indica centralis Erxleben) IN RELATION TO FOOD AVAILABILITY IN BORI WILDLIFE SANCTUARY, M.P., INDIA

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SUMMARY

The spatio-temporal heterogeneity of food supply and the consequent effects on food resource use and space-use patterns of the Indian giant squirrel (*Ratufa indica centralis*) in Bori Wildlife Sanctuary, was the focus of study. Territoriality, which may affect space-use patterns of individuals was of special interest. Climatic factors which may influence activity budgets and consequently the variability in seasonal space-use patterns are also discussed.

Based on individual variation in physical characteristics, I identified three focal animals (one male, one female and a sub-adult male) in the disturbed habitat (Bhainsa nala), and a male and female in the undisturbed habitat (Churnagundi nala) for whom data could only be gathered in winter. Therefore seasonal changes in space-use patterns is discussed for focal squirrels in the disturbed habitat. I kept a continuous record of behaviours during focal animal sampling. Home areas were calculated based on hourly locations taken from focal data. I gridded the area used by focal squirrels and recorded the vegetation parameters. The seasonal change in resource availability was monitored by phenological observations on all trees in the grids twice a month.

Squirrels in Bhainsa nala selectively utilised certain individuals of flowering and fruiting trees which was related to crop size. Squirrels included bark and leaves in their diet even when fruit resources were available. The resource use by squirrels in Churnagundi nala showed a marked difference from squirrels in Bhainsa nala in winter which was due to the poor availability of food.

Individual squirrels in Bhainsa nala showed variation in food species, food items used and the percent time spent feeding on each food item indicating that resource availability was not the same for all squirrels. No significant correlation was found between resource abundance and percent use of the item. Squirrels had overlapping ranges but were otherwise solitary. Many preferred resources were rare in the habitat, and the spatio-temporal

heterogeneity in food resources resulted in overlap between individuals at locally abundant food resources. Because of this heterogeneity, the defence of an exclusive area guaranteed of resources throughout the seasons is not possible. Therefore squirrel ranges overlapped, but encounters were avoided by spatial time sharing but when encounters occurred, overt aggression was seen. But at certain locally abundant resources which were located at the periphery of the home areas, squirrels tolerated each other by maintaining inter-individual distances (5-10m). The tolerance of conspecifics at these resources could also be related to the existence of dominance hierarchies which result in decreased overt aggression.

The intensity of use (time spent) decreased as the distance from nest increased for all squirrels. Squirrels made forays in search of food and in many cases foraging was in the peripheral areas of the range. The male's range showed overlap with the female's in winter which could be related to sexual activity.

Squirrels had a bimodal activity pattern in both seasons but bimodality was less pronounced in the winter since activity was distributed throughout the day when temperatures were more equable. Shift in onset and cessation of activity was observed with changing daylength. Time spent feeding in April was much less than in otherd months. Time budgets showed that in all months a higher proportio an of time is spent resting which could be due to heat or cold stres or time needed to digest food items eaten. in

Activity pattern of the squirrels in winter in Churnagundi nala were influenced by the low resource availability which resulted in long basking and resting periods and negligible time spent in feeding. Though occassional forays of short duration were made, no food was located by these forays. Thus squirrels adopted a strategy of conserving energy by minimizing their requirements by resting.

CHAPTER 1: INTRODUCTION

Resources such as food, shelter and mates are distributed in space, so space becomes an important resource (Gurnell 1987). An animal's use of space is closely linked to their social organization and species exhibit characteristic spacing patterns. Home range is considered to be the area over which an animal travels in pursuit of its daily activities (Jewell 1966). It includes all the environmental resources necessary for the animal's survival (Mitchell *et al.* 1977). It has been shown that the three most important determinants of home range size in 3 vertebrate orders are an animal's energetic needs (determined mainly by its body size), habitat productivity and patchiness in the distribution of resources (Mace *et al.* 1983).

The sudden availability of natural food sources results in shifts in home range use (Dunford 1970; Elliot 1978; Getty 1981; Snyder 1982). Factors such as patchiness and predictability of food resources may vary thus influencing the behavioural responses by an animal. Ranges may vary seasonally in response to changes in availability of food, shelter, cover and temporarily in the mating season. Therefore the patterns exhibited in the use of space by any animal is dependent to a large extent on food availability (Blackmore & Lishak 1985). An animal's movements are governed by the distribution of food resources (Burt 1940; Blair 1942; Mares *et al.* 1976). Therefore besides the consideration of amount of food available, the spatial distribution of food resources should also be taken into account. Food resources are also subject to temporal variations. Many plant species have irregular fruiting cycles (McClure 1966; Medway 1970, 1972; Smythe *et al.* 1982) and this may result in only a few tree species being in fruit and that too only a few individuals of a species (Frankie *et al.* 1974; Payne 1979; Raemakers *et al.* 1980; Leighton & Leighton 1983). During these lean periods a frugivorous mammal has to adapt by using alternate resources opportunistically or adopt other behavioural strategies (Borges 1989)

Another factor which affects space-use patterns of an animal is territoriality. A territory has traditionally been regarded as any defended area (Noble 1939). Current theory predicts that territoriality will occur when resources are limited and defendable (Brown 1964) as exemplified in primates (Mitani & Rodman 1979). However Kaufman (1983) has stressed that territoriality is a form of space-related dominance in which priority of access to resources rather than defence or exclusion is the critical component. This priority of access may be achieved through social interactions such as time-sharing or avoidance mechanisms which have been suggested to be important in mammalian territorial systems. It is clear that in such a contest for resources an individual's ability to secure adequate resources determines its survival and reproductive fitness (Kenward 1984). In the short-term, such behaviour affects the organization and spacing of ranges. Spatial heterogeneity of food, places many foraging constraints such as increased search and travel time, predation hazards (Blackmore & Lishak 1985) and in territorial species interactions with conspecifics who may limit access (Getty 1981b; Borges 1989). An animal's use of the habitat is also influenced by its needs for cover and shelter and the presence of nest trees and canopy continuity are important for squirrels. This may result in seasonal variations in individual space-use patterns. Climatic factors such as temperature and daylength may also cause seasonal changes in activity pattern which influence the space-use patterns of a mammal. This study is aimed at determining the space-use patterns of the Indian giant squirrel (*Ratufa indica*) in relation to food availability.

1.1 OBJECTIVES

This study deals with four aspects:

i) the seasonal and spatial patterns of food availability and how they influence resource use by squirrels.

ii) how the spatio-temporal distribution of these resources affects individual squirrel's space-use patterns.

iii) the effect of squirrels on each other's space utilization patterns.

iv) time budgets were also investigated in relation to resource use.

1.2 REVIEW OF LITERATURE

1.2.1 Ranging and space-use patterns:

Home range studies of squirrels in general has been extensively carried out mainly on ground and tree squirrels in North America (Elliott 1978; Hall 1981; Getty 1981a, 1981b, Kenward 1984). Similar studies on arboreal Asian squirrels are lacking. The concepts and methodology of home ranges have been reviewed by Brown 1966; Jewell 1966; Van Winkle 1975; Cooper 1978; Schroder 1979). Getty (1981b) summarizes some of the problems with home range studies. One of the major criticisms is the representation of home ranges as static maps which does not reflect actual space-use patterns. Many parts of an animal's range may not be used except for travelling through. The use of the minimum convex polygon which is extremely sensitive to forays has been criticised because of this reason. Van Winkle (1975) has developed a 'probabilistic model'. " Use intensity is defined as the probability distribution of spatial occupation over some specified time period" (Van Winkle, 1975). Models have been developed which assume various multivariate normal distributions (Calhoun & Casby, 1958; Jennrich & Turner, 1969; Koeppl *et al.*, 1977). These models show the actual occurrence of high use 'core areas'. Mammal home ranges are not homogenously used. Differential use causes heterogeneity. This heterogeneity of use is not evident when only a map of the range is given by using the convex polygon. The presence of a nest or a central point brings in the distance factor for the animal. Even if distance itself is not a constraint for the animal, the presence of conspecifics, predators and the patchy distribution of resources results in differential use of the home range (Getty 1981b).

As mentioned before, many species have irregular fruiting cycles and thus arboreal frugivores are often faced with irregular patterns of fruit availability. Plant species also often occur at low densities (especially in tropical rain forests) so many food species are rare and dispersed (Payne 1980). Ranging patterns of arboreal frugivores such as *Ratufa* is therefore likely to be determined by dispersion of fruit sources.

Territorial aggression has been viewed as leading to competition (Getty 1981a). Burt (1940) observed that though chipmuks had overlapping territories when individuals encountered each other aggression occurred. Dunford (1970) noted that intruders who got chased away from a resource invariably returned when the resource defenders had left. Even though this may not exclude an individual from total access to space the fact that territoriality (i.e. aggression from neighbours) influences the space-use patterns of an individual, points to the possible existence of interference competition. Getty (1981a) raised the question whether the interference with timing of access to resources affects the total access. This will be one focus of discussion in regard to this study.

Any study of space-use patterns needs to recognize and incorporate the fact that time is an important factor influencing an animal's use of space. Its activity patterns can be viewed as the fourth dimension of a single phenomenon (Hall 1981). Activity rhythms in squirrels are said to have an endogenous basis as in most other animals (Daan & Aschoff 1975). But seasonal variation in daylength and food supply have been found to exert a great influence on activity patterns (Tonkin 1983). Breeding behaviour especially in lactating females could affect their activity patterns (Tonkin 1983). A proximate explanation for bimodality and seasonal variation in activity patterns in mammals has been given Daan & Aschoff 1975; Pittendrigh 1974). They postulated the existence of a dual oscillator system: a morning oscillator speeded up by light and locked onto dawn and an evening oscillator, slowed down by light and locked onto dusk. The onset of activity would be linked to the morning oscillator in day-active animals. The cessation of activity would therefore correspond to the evening oscillator in day-active animals. The existence of these systems in the circadian rhythm is indicated by the usual bimodal activity pattern (Ferron 1983).

1.1.3 The Indian Giant Squirrel

General description and distribution: *Ratufa indica* belongs to the Order Rodentia, Family Sciuridae, sub-family Sciurinae. The genus *Ratufa* includes the world's largest tree squirrels with four species belonging to the Indo-Malayan realm. Three species occur in India. The black giant squirrel (*R. bicolor*) ranges through the eastern Himalayas, Burma, southern China, Indo-China, Thailand, Malaya and the islands of Sumatra, Java and Bali. The grizzled giant squirrel (*R. macroura*) occurs in Sri Lanka and has a restricted distribution in southern India (Joshua 1992). Three races are found in Sri Lanka and only one race *dandolena* is found in India. The Malabar or Indian giant squirrel (*R. indica*) occurs in peninsular India and extends northward upto Bihar and Orissa. Seven geographical races of *R. indica* have been described viz. *indica, maxima, benghalensis, dealbata, superans, elphinstoni and centralis.* The fourth species is the cream-colored giant squirrel (*R. affinis*) occurring in southern Thailand, Malaya and in Sumatra, Borneo and other islands. *R. bicolor* and *R. affinis* are sympatric in some parts of their range and are primarily rain forest animals. *R. indica* and *R. macroura* are not sympatric in any part of their range. *R. macroura* is essentially an animal of dry deciduous habitats.

The Indian giant squirrel inhabits the deciduous, mixed deciduous and moist evergreen forests of peninsular India, south of Ganges (Prater 1980). Variations in colour forms have led to classification into local races. In peninsular India the darkest form of giant squirrel is found in the moist evergreen forests of the Western Ghats, palest in the dry open forests of the Dangs; with forms intermediate in colour inhabiting dry deciduous and mixed deciduous forests suggesting that differently colored geographical races are in some way correlated with local physical and climatic differences (Abdulali & Daniel 1952). This species is not as endangered or rare as the other two *Ratufa* species in India, All species of *Ratufa* are on Appendix II of CITES and Schedule II of the Wildlife Protection Act of India, 1972.

Notwithstanding a few recent studies, the ecology of Asian squirrels has been little studied and literature is scarce. Payne (1979), studied a guild of tree squirrels in Malaysia which included *Ratufa bicolor* and *R. affinis* and some other species. Mackinnon (1978) studied a similar guild. Whitten (1981) studied ecological separation of three arboreal squirrels in Indonesia. The literature on squirrels in India was largely anecdotal till recently. Studies on the genus *Funambulus* has been carried out (Purohit *et al.* 1966; Prakash *et al.* 1968). The ecology of the endangered grizzled giant squirrel has been studied (Joshua 1992). A descriptive study of the Malabar giant squirrel was carried out in Parambikulam Wildlife Sanctuary (WLS) (Ramachandran, 1988). A comprehensive study of the Indian giant squirrel has been carried out which focused primarily on nutritional factors and foraging ecology (Borges 1989).

Diet and food habits: *Ratufa indica* has been found to be a facultatively frugivorous, generalist herbivore. Seeds constituted the major portion of the daily diet whenever they were available. In non-fruiting periods, young and mature leaves, flowers, pith and bark were alternate food sources (Borges, 1989). Food caching has not been observed in *Ratufa* spp. The spatio-temporal fluctuations of food resources affects their foraging strategy resulting in them being a facultative generalist frugivore (Borges 1989).

Social organization: Home range size has been estimated for grizzled giant squirrel (Joshua 1992), for *R. bicolor* and *R.*

affinis (Payne 1980) and for Indian giant squirrel by Borges (1989) and Ramachandran (1988). These estimates vary widely and Ramachandran's estimate is for only one animal.

Giant squirrels have been reported to be territorial with individuals being spatially segregated to some extent (Borges 1989) They are solitary animals, though young may stay with the mother upto one year (Renee Borges *pers. comm.*). Gestation time has been reported to be 5 weeks (Borges 1989) with young attaining half the adult size within two months of emergence. Aggression between individuals has been noted (Ramachandran 1988; Borges 1989). Borges (1989) found *Ratufa indica* to have a system of overlapping ranges in which individuals used avoidance tactics to reduce temporal overlap. Thus a mechanism of time-sharing in giant squirrels achieved by the use of vocalizations and scent-marking has been reported by Borges (1989).

CHAPTER 2: STUDY AREA

2.1 LOCATION

Bori Wildlife Sanctuary (WLS) lies in the Satpura hill ranges, bordering the Narmada valley and forms the catchment area of the Denwa river. The sanctuary is situated between 22^{0}19’28" to 22^0 30’18" N latitude and 77^{0}56’40" to 78^{0}20’40" E longitude in the south-eastern part of Hoshangabad district in Madhya Pradesh, (Fig.1) being bounded on the north by the hill ranges of the Mahadeo, the Tawa river on the west, Betul district boundary on the south and Chhindwara district to the east. The Denwa river flows in the north-east. The Tawa reservoir is located at the confluence of Tawa and Denwa rivers. Bori WLS is the oldest Reserved Forest in India having been declared in 1865 and was declared a Sanctuary in 1972 (Gangopadhyay 1985). The Sanctuary occupies an area of 485.72 sq.km. Bori WLS, Pachmarhi WLS and Satpura National Park (N.P.) together form a conservation unit in the Satpura hills. Satpura N.P. was created out of parts of Bori WLS in 1977.

2.2 GEOMORPHOLOGY

The altitude varies from 305m to 1045m above m s l and the topography is hilly with steep ridges in the east to flat and undulating in the west. The rocks of these forests belong to the upper and lower Gondwana series with sandstone and limestone being the main types. The underlying rock is basaltic sheet of Deccan Trap (Gangopadhyay 1985).

2.3 CLIMATE

Bori WLS has three distinct seasons, winter (November to February), summer (March to mid-June). The rainy season starts by mid-June and lasts till mid-September. Average annual rainfall at Bori is recorded to be 2067.5mm ranging from 1188 to 3273mm. Winter rains also occur sometimes in January and February. Rainfall along with hailstorm occurred on six days during the study period in spring between February 26 and March 4. Mean maximum temperature varies from 26.5^{0}C in January to 42.15^{0}C in May. Mean minimum temperature varied from 11.8^{0}C in January to 27.1^{0}C in May. Temperature data recorded during the study period is given in Table1.

2.4 VEGETATION

The principal plant communities are dry to moist teak-bearing forests and poor to good quality miscellaneous forests. The major forest type of Bori is 3 B/CI(b) = South Indian moist deciduous teak forest (Champion & Seth 1968). The main associates of teak are *Terminalia* spp., *Adina cordifolia, Anogeissus latifolia, Diospyros melanoxylon, Aegle marmelos* and *Lagerstroemia parviflora*. Forty eight percent of the total area of the sanctuary is under workable bamboo forests, the only species worked being *Dendrocalamus strictus* (Gangopadhyay 1985). Rare species in the Sanctuary include clumps of *Bambusa polymorpha*, sal (*Shorea robusta*) trees and *Thysanolaena maxima*, a rare grass species.

2.5 FAUNA

The Sanctuary has a diversity of wildlife. Among the Carnivora, are tiger (*Panthera tigris*), leopard (*Panthera pardus*), striped hyaena (*Hyaena hyaena*), dhole (*Cuon alpinus*), jungle cat

(*Felis chaus*), jackal (*Canis aureus*), sloth bear (*Melursus ursinus*) and the aquatic carnivore - the smooth coated Indian otter (*Lutra perspicilliata*). The ungulates found include gaur (*Bos gaurus*), sambar (*Cervus unicolor*), chital (*Axis axis*), barking deer (*Muntiacus muntjac*), chousingha (*Tetracerus quadricornis*), nilgai (*Boselaphus tragocamelus*), and wild pig (*Sus scrofa*). Chinkara (*Gazella gazella*) is also reported. Mouse deer (*Tragulus memmina*) also occurs. The other mammalian species include pangolin (*Manis crassicaudata*), ratel (*Mellivora capensis*), two civet species, the small Indian civet (*Viverricula indica*), and palm civet (*Paradoxurus hermaphrodites*), porcupine (*Hystrix indica*) and rufous-tailed hare (*Lepus nigricollis ruficaudatus*). The two primate species are common langur (*Presbytis entellus*) and rhesus macaque (*Macaca mulatta*). Other arboreal mammals are the central Indian subspecies of the Indian giant squirrel (*Ratufa indica centralis*) and the large Indian flying squirrel (*Petaurista petaurista*).

Two hundred and fifteen bird species have been recorded (Ashwini Pai, *pers. comm.*) Some important species include grey jungle fowl (*Gallus sonneratii*), red jungle fowl (*Gallus gallus*), Malabar pied hornbill (*Anthracoceros coronatus*), and Malabar whistling thrush (*Myiophonus horsfieldii*). Two avian predators of giant squirrel were also recorded here i.e. crested hawk eagle (*Spizaetus cirrhatus*) and crested serpent eagle (*Spilornis cheela*). Reptiles include monitor lizard (*Varanus benghalensis*), python (*Python molurus*), common krait (*Bungarus caeruleus*) and a small population of marsh crocodiles (*Crocodylus palustris*).

2.6 BIOTIC PRESSURES

Bori WLS has 17 forest villages occupying an area of 3734.2 ha. The population of these villages is around 3500. Cattle population is around 7500. The villagers are cattle-rearing Goulis and the tribal Gonds and Korkus. They collect deadwood for firewood, some bamboo and timber are allowed to be collected for construction and fencing. Minor forest produce collection is a source of income involving collection of *Mahua* flowers, *Buchnania lanzan* fruits and honey. Cultivation has been allowed in the low-lying drawdown areas of the Tawa reservoir. Forestry operations, which used to be a major source of employment, have ceased since 1992.

2.7 INTENSIVE STUDY AREA

Two patches of riverine habitat with a population of giant squirrels were selected as study sites. The squirrels also used the adjoining deciduous forest. Though the vegetation composition of the two areas were similar, they differed in the degree of disturbance. The riverine habitat along Bhainsa Nala was subject to disturbance due to the presence of Churna and Siridhana villages nearby. On one side of the nala, for a length of 1.5 km, the deciduous patch had been cleared for a nursery set up by the Forest Corporation in 1975. The area was used for preparation of nursery beds and construction of buildings. During the study period, work was going on in the nursery and human presence and noise was continuous. Cattle also used the area. Two diesel pumps were at times operated throughout the day. Canopy gaps have occurred due to the previous felling of trees. Even 15m from the riparian area, canopy continuity is lacking in many areas. The intensive study area was approximately 9.48ha. The location of Bhainsa nala is given in Fig.2.

The other study area was a relatively undisturbed riparian habitat along Churnagundi Nala, which is an offshoot of Bhainsa Nala. This study area was located in Satpura N.P. The presence of cattle was also noted here but it was largely free from human disturbance except for occasional tourists and pilgrims. No forestry operations have been carried out here.

In both the areas, the dominant riverine tree species were *Terminalia arjuna* (Combretaceae), *Syzygium cumini* (Myrtaceae), and *Mangifera indica* (Anacardiaceae). Undergrowth was confined to dense patches of regenerating *Syzygium*. In the deciduous area near Bhainsa Nala, the dominant tree species were *Terminalia bellerica*, *T. tomentosa* (Combretaceae), *Careya arborea* (Myrtaceae), *Madhuca indica* (Sapotaceae) and *Aegle marmelos* (Rutaceae) with *Butea monosperma* (Leguminoseae) and *Saccopetalum tomentosum* (Anonaceae) being the most common middle storey trees. In Churnagundi, dominant species were *Madhuca indica*, *T. bellerica*, *Lannea coromandelica* (Anacardiaceae), *C. arborea* and *Scleichera oleosa* (Oleaceae). Common middle storey trees were *S. cumini* and *S. tomentosum*. Shrub layer was practically absent with scattered *Helicteres isora* (Sterculiaceae), saplings of *Wrightia tinctoria* (Apocynaceae), bamboo (*Dendrocalamus strictus*) and *Murraya koenigii* in some patches near Bhainsa Nala. Along Bhainsa nala, dense patches of *Lantana camara* were present. *Phoenix acaulis* (Palmae) was common in the deciduous area in Churnagundi. Two common climbers were *Ventilago calyculata* (Rhamnaceae) and *Clematis triloba* (Celastraceae).

CHAPTER 3: METHODS

3.1 FIELD METHODS

3.1.1 Focal animal sampling:

To obtain information on space-use patterns, behaviour and time budgets, I identified 3 squirrels (1 male, 1 female and a sub-adult male) in Bhainsa nala (disturbed habitat) and a male and a female in Churnagundi nala (undisturbed habitat). Individuals were identified mainly by ear profile, facial and belly markings and length, color and shape of tail. On each observation day, I located a squirrel as it left its nest at dawn and followed it until it entered its nest at dusk. A continuous record of behavioural states and events was maintained (Altmann 1974). The behavioural states were feeding, resting and moving. Activities such as aggression, scent marking, and defecating were regarded as events. The list of recorded behaviours is included in Appendix I. Transitions between states and events were timed to the nearest second using a digital watch. I attempted to follow each focal squirrel twice a month. Data was gathered for two seasons- part of winter (mid December-February) and part of summer (mid March- April).

Though I attempted to follow each animal twice a month, problems were faced in locating focal individuals. At Bhainsa nala, a focal male could not be located after following it for two days in December. Another male was followed instead of it. At Churnagundi nala, behavioural data for summer could not be obtained for both the squirrels. The focal female (Bhainsa nala) gave birth to a pup which could also be observed in summer when follwing the female. During focal animal sampling, I recorded the following

1. Time
2. Activity
3. Quadrat number
4. Height of animal location
5. Food species
6. Food item
7. Phenology of food item consumed
8. Ambient temperature

3.1.2 Quadrat laying:

The entire area used by focal individuals was gridded by laying quadrats of 15m by 15m by using compass bearings along the north-south and east-west directions. On any observation day if a squirrel used an area which had not been gridded, quadrats were laid in these areas at a later date.

3.1.3 Tree mapping:

All trees in the quadrats laid were mapped by measuring the two distances from the grid intersection points on the north-south axis to the tree bole. Trees were marked by nailing tin tags to the bole at eye level. The quadrat number, tree species and number were painted on the tags by using bright oil paint enabling them to be read at a distance.

3.1.4 Phenology:

Within the intensive study area, all trees in every quadrat used by the focal squirrel were monitored for phenological changes twice a month. The number of trees in the following phenophases were counted, i.e. sprout leaves, mature leaves, senescent leaves, leafless, whether flowering or not, unripe fruit, semi-ripe fruit and ripe fruit (Borges 1989). Phenology of shrubs was not quantified since undergrowth was largely absent and no instance of a squirrel using shrubs was recorded. Two climbers that were present in both areas were a minor food resource. Their phenology was not monitored, though when use occurred, the phenology of the part eaten was noted. Thus by this method, a total count of the number of trees of each species in a particular phenophase was obtained in both areas on a monthly basis.

3.1.5 Territories and home ranges:

The criteria and methods adopted by Borges (1989) to demarcate ranges and territories of focal squirrels were followed. To obtain information on the degree of overlap and the organization of squirrel home ranges, the presence of other squirrels were also noted while observing the focal animal. A tree was considered to be outside an individual's territory i) if the squirrel was chased away from a food tree, ii) if it left a food tree with a partially consumed food item to feed some distance away on the approach of another squirrel, iii) if it exercised caution in approaching or feeding in a tree, or iv) if it waited near a feeding tree for another squirrel to leave the tree before entering (Borges 1989).

3.1.6 Aggression:

Aggression was a behaviour of particular interest, as it affects organization of the home ranges and the density of animals, therefore every aggressive encounter was timed. The locations (quadrat and tree numbers) and distances moved by the aggressor and recipient were also recorded. Frequency of aggressive interactions for each observation day was obtained by counting each interaction separately. If during an interaction, the recipient, later became the aggressor, it was counted as two separate aggressive interactions. The daily frequency and duration of aggression were determined.

3.2 Analytical methods :

3.2.1 Tree species composition and relative abundance:

I calculated the relative abundance (%) of tree species in the gridded area in the two habitats. I calculated Sorenson's index of similarity (IS) (Mueller-Dombois & Ellenberg 1974) to compare percent similarity among tree species in the two habitats. IS is computed as: $IS = 2C/A+B \times 100$

where C is the sum of species common to both areas and A+B is the total number of species in the two areas.

3.2.2 Food dispersion:

To determine the distribution of flowering and fruiting trees in Bhainsa nala for each month, I calculated a variance to mean ratio using the number of flowering and fruiting trees in each quadrat. The variance to mean ratio is usually referred to as the index of dispersion (Ludwig & Reynolds 1988). However, a number of variants of this ratio have been proposed to measure the degree of clumping (including index of clumping (IC) and Green's index. The index of dispersion is:

$$ID = \frac{s^2}{x}$$

where s^2 is the variance and x the mean. It varies from 0 for uniform, 1 for random and n (sample size) for maximum clumping. But in terms of measuring degree of clumping it is not a useful index. David & Moore (1954) proposed a modification of ID they termed the index of clumping : $IC = (s^2/x) - 1 = ID - 1$

IC is equal to 0 for random, -1 when there is maximum regularity, and n-1 when there is clumping. But a further modification has been proposed since it is not a useful comparative measure as it is dependent on n. Green (1966) modified IC, independent of n, i.e. Green's index: $GI = \underline{IC}/\ n-1$

GI varies between 0 for random and 1 for maximum clumping. I used all three indices.

3.2.3 Food resource use:

Resource use by squirrels will only be discussed in terms of percent time spent feeding (TSF). This has been used as an index of food preference. TSF is a good estimator of relative intake of foliage of different plant species but either over-estimates or under-estimates the intake of seeds and fruits (Iwamoto 1978). Time spent on each food species may not necessarily indicate the importance of that species in the diet since processing and handling certain food items such as bark may take a relatively longer time; inspite of this, percent time spent on bark feeding in each month was less than that for non-bark items which may take less time to process. Therefore a comparison of time spent between different food items would have been incorrect. Therefore preferences were calculated only for the fruit and floral resources.

3.2.4 Selection ratio:

To calculate the relative preferences of fruit and floral resources I used selection ratio which has been used as an index of relative preference of food parts (Clutton-Brock 1977). Selection ratio is calculated as:

$$SR = \frac{Pi}{Ai}$$

where Pi = percent time spent feding on food item 'i'

Ai = relative availability of the item 'i'

Healy (1971) has categorized these preference indices or ratios as high (> 1.5), medium (0.75 to 1.5), or low (< 0.75). The selection ratio for each floral and fruit species was calculated separately for each month for the three squirrels.

To correlate foraging strategy with resource availability, the spatio-temporal patterns of food resource availability for squirrels need to be determined. This was done in a semi-quantitative manner following the method of Heithaus *et al.* (1975). Only floral and fruit resources were considered for calculating the index for each species . A rank of 1-9 was assigned to each flower and fruit resource according to its relative density (rare, common, or abundant) and dispersion pattern (dispersed, moderately clumped, or clumped) as determined by the distribution and number of trees of each species. An overall index of resource abundance for each species was calculated by multiplying its rank by the length of its flowering or fruiting season.

3.2.5 Activity budgets:

For determining activity pattern, each hour was sampled at 10 minute intervals by scoring squirrels as inactive or active as described by Tonkin (1983). Squirrels inside the drey as well as resting outside were scored as inactive and squirrels outside the drey for all other activities were scored as active. For each hour of the day, the sum of active points was expressed as percentage of the sum of active and inactive points, giving an estimate of hourly percent activity.

Percent time spent in foraging (including search and handling times), resting (both inside and outside drey) and moving was calculated by treating the continuous data to 2 minute scan sampling to obtain the percent time spent on the three activities, per month for each squirrel. Percent time spent in other behaviours were not calculated separately for each behaviour but grouped together as others.

3.2.6 Home area determination:

Due to lack of adequate sampling days spread over the seasons, I estimated home area instead of home range by taking hourly locations from focal data, to ensure a certain degree of independence. The term 'home area' has been used in case of inadequate sample sizes by Emmons (1983).

As the sampling rate approaches continuous recording, the fact that there are no independent samples has statistical problems (Dunn & Gipson 1977). As Getty (1981b) has pointed out, in case of continuous sampling it is necessary to argue that the sample is representative of longer time periods.

The use of circular or ellipsoid range models for determining squirrel ranges has been criticised since assumptions of such models are violated (Don 1983), therefore convex polygons were used to estimate range sizes. Home area was determined by joining the outermost locations at which each individual was seen (Mohr 1947).

3.2.7 Use intensity of area in relation to drey:

To determine whether the squirrels spent lesser time away from the nest tree, I categorized distance classes in 15 m intervals away from the nest tree grid and counted the number of grids which were in each distance class. The monthly mean percentage time spent in each quadrat was calculated and pooled for each distance class.

CHAPTER 4. RESULTS

4.1 Food availability and phenology of food species:

In Bhainsa nala, *Butea monosperma* was the most abundant species forming 15.7% of all tree species followed by *T. arjuna* which formed 13% of all tree species. *Saccopetalum tomentosum* and *Syzygium cumini* were the two next abundant species forming 12% and 11% respectively in Bhainsa nala. *Madhuca indica* was the most abundant species in Churnagundi nala. The relative density of each species in the two areas is given in Appendix IIa & IIb.

As a result of the way in which the phenology data was collected every month, some error in determining the exact number of fruiting trees may be there but I am confident that in general, fruiting trees were not missed in the study area. The length of the flowering and fruiting periods of fruit and floral resources during the study period is given in Fig. 14a & b. Fruit was available at low levels throughout the study period in Bhainsa nala. 3.84% (31) of all trees (n=806) were in fruit in December- January. Of these, 21 (67.7%) fruiting trees were of *Terminalia arjuna*, the other species being *Terminalia bellerica* - 4 (12.12%), *Bridelia retusa* - 3 (9.09%) and *Phyllanthus emblica* - 3 (9.09%). The total number of fruiting trees declined slightly to 29 (3.59% of all trees) in February since *Terminalia bellerica* trees were devoid of fruit by middle of February. Fruiting trees of *Terminalia arjuna* declined from 21 in December-January to 20 in February and finally to 8 in March. *Terminalia arjuna* fruits were not available in April. In the first 15 days of March, 3 fruiting trees of *Aegle marmelos*, 1 each of *Ficus religiosa* and *Ficus glomerata* were available besides the fruiting *T. arjuna*. All these fruiting trees had unripe fruits.

Three trees of *Bridelia retusa* were also in fruit but the size of the fruit crop was small. Towards the end of March, the fruits of *Bombax ceiba* became available. In April, the total number of fruiting trees was the highest in the three months (41) but this was largely due to the large number of fruiting trees of *Butea monosperma* with unripe pods (31). The fruits of *Ficus religiosa* and *Bombax ceiba* had ripened by this time. Four trees of *Mangifera indica* with unripe fruit were also available.

In winter, mature leaves were the predominant leaf phenophase on all 41 tree species recorded in the study area. But in *Syzygium cumini*, an evergreen species, sprout leaves appeared by February. Sprout leaves also appeared in evergreen species such as *Mangifera indica* in March. For the other tree species, the proportion of senescent leaves in trees increased steadily and mid-March to April was the peak of leaf fall. In many tree species such as *Terminalia bellerica, Saccopetalum tomentosum, Terminalia arjuna,* and *Butea monosperma*, sprout leaves only became available in mid-April.

In December-January, only a few trees of planted exotic species, *Peltophorum ferruginea* and *Acacia auriculiformes* were in flower. In February, 2 trees of *Buchnania lanzan* and 4 trees of *Bombax ceiba* were in flower. Flowering peaked in March-April when 8-9 food species were in flower. Sixty-five trees in March and 123 trees April were in flower. Some of the other species in flower were *Butea monosperma, Syzygium cumini, Mangifera indica,* and *Careya arborea* which flowered only in April.

In Churnagundi nala, only 6 trees out of 459 trees were in fruit in January. Out of this 3 fruiting trees were of *T. arjuna*. The number of trees in fruit declined to one in February. Though phenology data was collected in March too, it will not be discussed since no focal animal data on the animals could be gathered.

4.1.1 Inter-individual variation in flowering/fruiting phenology:

Due to the method of phenology data collection a few trees in flower and fruit could have been missed. Even after accounting for that, only a few trees of each species bore fruit. For example, only 23 out of 106 trees of *T. arjuna* were in fruit in January (21.8%). Four out of 19 trees of *T. bellerica* bore fruit. This was the case for most other species in the area. Ten out of 21 trees of *Careya arborea* flowered.

4.2 Food dispersion:

Variance was greater than mean in all three months signifying clumped distribution of fruiting and flowering trees. The ID values in all the three months varied from 1.2 to 1.3, therefore near random distribution is signified. GI values (0.001) also signified a distribution lying between random and clumped, being closer to random distribution. The distribution of fruiting *Terminalia arjuna* was also close to random distribution (GI value = 0.004).

The indices of resource abundance for fruit resources ranged from 1 in *Bombax ceiba* to 28 in *T. arjuna* with an average value of 7.75. For floral resources, the values ranged from 3 in *Bombax ceiba* to 16 in *Syzygium cumini* and *Butea monosperma* with an average value of 8.44. (Table 8). The indices of resource abundance for different species of flowers and fruits were compared to the percentage use for each resource and no correlations were found (Pearson's correlation=0.57)(Fig. 15).

4.3 Food resource use:

Based on percent time spent feeding (TSF), fruit (57.88%) appears to be the major food source for all squirrels during the study period in Bhainsa nala. The monthly percent TSF on different food item classes is given in Table 2b. When squirrels are considered separately, there was a variation in the food species as well as the food items consumed. Monthly means of %TSF on food items also showed variation between individuals (Table 2a).

In December-January, the fruits of *T. arjuna* and *T. bellerica* formed the major fruit source. The squirrels were actually feeding on seeds of both species.

The consumption of *T. arjuna* seeds ranged from 44.66% to 62.19% of TSF with a mean of 52.38%. By the middle of February, most *Terminalia bellerica* had no fruits, so *T. arjuna* was the only major fruit source with 52.4% of the TSF on fruits being on *T. arjuna*. *Bridelia retusa* was important for the adult male (AM) (25.15% of TSF) being next in importance to *T. arjuna*. The adult female (AF) in February had access to unripe fruits of *Aegle marmelos* (3.46% of TSF) of which only the pulp was eaten. *Phyllanthus emblica* (1.42%) also formed a fruit source for this squirrel.

Flowering trees of *Bombax ceiba* formed an important food resource for the squirrels (n= 9 out of 12 observation days) in Bhainsa nala area in February-March. One of these trees which had abundant flowers was fed on exclusively, and as a result this tree hardly had any fruit in March end. Squirrels, therefore, used an adjacent tree which had a larger fruit crop. The sprouting flower buds of *Bombax ceiba* formed 11.04% of the TSF for the AF and sub-adult male (SAM) in February and 15.10% of the TSF in March. The AF spent only 5.24% of the TSF on *Bombax ceiba* flowers in March. The AF consumed the fruits of one *Bombax ceiba* which fruited earlier than the others in March. Flowers became an important component of the diet mainly in mid-March to April when 8-9 species were in flower. The highest use of flowers by the AF was observed in April when 62.26% of the TSF was spent on consuming flowers. The nectar and fleshy ovary of *Careya arborea* were eaten for 36.58% of the TSF on flowers. This was the only instance where TSF on flowers exceeded TSF on fruit. The AF spent only 5.32% of the time feeding on fruits which included the unripe pods of *Butea monosperma* and the unripe fruits of *Mangifera indica*.

At this time, for the two male squirrels, fruits still remained a major component of the diet (Table 2a). The AM had a fruiting *Ficus religiosa* tree in his range which took up 70.09% of the TSF. TSF on flowers was 17.42% in April for the AM.

For the SAM, *Bombax ceiba* was the main fruit source (48.7%) in April. Flower feeding took up 39.8% of the TSF with *Careya arborea* flowers taking up 28.15% of the TSF on flowers.

Squirrels fed on sprouting and mature leaves of *Mangifera indica*, *Syzygium cumini* and *Ficus glomerata* and mature leaves of *Terminalia arjuna* and *Tamarindus indica*, but leaves never formed an important component of the diet (Table 2b) except in April for the AF (23.14%).

Bark feeding varied from 12% in February to 21.29% in March to a low of 4.17% in April. The bark of species such as *Terminalia arjuna*, *M. indica*, *T. bellerica*, *C. arborea* and *Mangifera indica* were fed on. When individual squirrels are considered separately bark feeding varied from 6.8% (SAM) to 21% (AF) in February. In March it varied from 17.71% for the SAM to 27.96% for the AF. In

April it ranged from 1.37% for the AM to 8.38% for the AF. For all three months the AF spent a higher proportion of time feeding on bark than the two male squirrels.

In the undisturbed habitat, where only winter data could be gathered, resource availability was poor compared to that of Bhainsa nala with only 1.3% of trees in fruit. The adult male (BEM) had only 3 fruiting trees of *Terminalia arjuna*, 1 of *Ficus benghalensis* and 2 of *Phyllanthus emblica* in his range in January. By February, only one *Phyllanthus emblica* remained in fruit. In January, when fruits were available, TSF on fruit was 56.48%. Bark feeding accounted for 32.46% of TSF. In February, TSF on bark amounted to 86.16% and fruits accounted for only 3.9% of the TSF. The female in this area was observed for two days in winter and had 2 fruiting trees, 1 each of *Bridelia retusa* and *Terminalia chebula* in her range. No squirrel was observed feeding on the latter species. Seventy-three percent of TSF was on bark which was mainly of *Madhuca indica* and *Terminalia bellerica*. Nearly fifteen percent of the TSF was on fruits of *Bridelia retusa*. This squirrel's range was approximately 100 m away from the riparian area. However it cannot be called a truly deciduous forest because of the presence of large numbers of *Syzygium cumini* trees. Tree species composition was similar to that of Bhainsa nala except for the absence of *Terminalia arjuna* in the female's area. I calculated Sorenson's index of similarity (IS) which indicated 76.92% similarity in tree species between the disturbed and undisturbed habitat.

The monthly selection ratios for different floral and fruit species for each individual in Bhainsa nala is given in Table 3.

Time spent feeding in a grid could not be correlated with food availability in a grid since I did not estimate relative abundances of different phenophases. I only had a count of the number of fruiting and flowering trees in each grid and not the quantity of fruit/flower in each tree. Therefore no food availability index could be calculated. The quadrats used for feeding by the 3 focal individuals is shown in Fig. 12a-12c.

4.4 Home area:

The overall home area for the three squirrels in Bhainsa nala varied from 1.137 ha for the AM to 0.97 ha for the AF and 0.91 ha for the SAM with a mean home area of 1 ha. The male in Churnagundi nala had a range size of 2.03 ha in winter (Fig. 3-7). For the male in Bhainsa nala, winter range (0.923 ha) was larger than the summer range (0.504 ha). Percent overlap in winter and summer ranges was 28.45%. His range also overlapped with the AF's range in winter (9.26%) but there was no overlap in summer. For the AF, winter range (0.48 ha) was smaller than the summer range (0.917). Overlap between winter and summer ranges was 39.33%. The SAM also had a smaller range in winter compared to summer with overlap being 26.37%. The AM and SAM's ranges overlapped both in summer (8.24%) and winter (5.74%). Coefficient of variation between individual home areas in summer was 28.8%, indicating that home areas did not show vary much between squirrels of different age/sex classes. Coefficient of variation for home areas in winter was much greater (53.85%) between the three individuals. There were no significant differences in home areas between seasons for the three individuals (Mann-Whitney U two-tailed test, U=3, p=.70).

The monthly ranges used by squirrels in terms of quadrats used are given in Table7. The overall range sizes were smaller than the home areas calculated by taking locations. The cumulative quadrats used were compared with the number of scanning days. For the AF, 95% of the total area was covered after 5 scan days and the time-area curve appeared to stabilize (Fig.11). The time-area curve for the AM levelled earlier with 82.35% of the total area being measured in one day itself and 92.15% being covered by the second day. Only 58.33% of the total area was measured by the fifth day for the SAM the curve appeared to stabilize only on the sixth day with 94.44% of the area being covered. For the AM in Bhainsa nala, 81.15% of the area was covered by the third day.

4.5 Territoriality:

Squirrels had overlapping ranges but were solitary. Territoriality was seen in terms of aggressive encounters related to fruit feeding, other food feeding or territorial defence. It should be noted that there were other squirrels in the study area which were not focal animals but these individuals were frequently observed and their ranges also overlapped with those of the three focal animals. At least three other individuals are known to have their ranges overlapping with my focal animals. One of these was an adult female with a pup. Her nest was 30m away from the nest of my focal sub-adult male. I believe that the sub-adult male could be the previous year's pup of this female. His range completely overlapped with hers. I also observed an interaction in which this adult female, the juvenile pup and the sub-adult male rested together on her nest tree in April. Allogrooming was also observed between the female and the sub-adult male. The adult female tolerated this sub-adult male's presence near her pup whereas she was seen to have been aggressive to other males. However in March, she had also shown aggression towards the sub-adult male if he got too close to the pup and the sub-adult male also avoided the juvenile pup.

There was considerable inter-individual overlap between ranges. In spite of this, squirrels tolerated each other at times, and whenever aggressive encounters occurred it was usually at or near a food source. Individuals also showed avoidance behaviour by moving away from a tree on seeing the presence of another squirrel. Therefore squirrels were at times excluded from food sources, but on occassions a squirrel re-entered or used a feeding tree after the dominant individual or territory holder had left.

In February and March, especially in the latter month, when fruiting trees were scarce, 4-5 squirrels were usually observed feeding together on one fruiting *Terminalia arjuna* and a flowering *Bombax ceiba*. These food sources were at the periphery of ranges of all the three focal animals. The seasonal mean duration of aggression and daily frequency of aggression is given in Table 5a & 5b. The duration of aggression was the least in April (101 seconds per day), 158 seconds per day in March and 159.28 seconds in February. Daily frequency of aggression ranged from 2.33 interactions per day in March to 1.66 in April and 1.57 in February. The duration and daily frequency of feeding aggression, fruit feeding aggression and general aggression is also given in Table 5a & 5b. Out of 10 aggressive interactions observed in April, 5 interactions were related to fruit feeding aggression. In March, only 3 interactions were related to fruit feeding.

4.6 Use intensity of an area in relation to drey:

Fig.13 represents the actual distributions of use intensity of grids for the 3 months for the 3 animals. All the focal squirrels tended to spend more time near their nest tree. As distance from the nest tree increased, time spent decreased. In December, the AF spent 84.4% of the total time within 0-15 m distance class. Nearly fifty-eight percent of the total time was spent in the nest tree grid only. The maximum distance moved in December was within 60 m from the nest tree. This is in contrast to the situation in February when maximum distance moved was 240 m from the nest tree. In February too, the nest tree grid was the most highly used in terms of time spent (62.15%) with total time spent in the 0-15 m being 67.15%.

The AF had shifted her nest to another T. *arjuna* tree in March. In March, the maximum distance moved was 210 m from the nest tree and time spent in the 0-15 m distance class was 48.55% which is less than in the other months. Nineteen percent of the time was spent in the 136-150 m distance class. In April, though maximum distance moved was 195 m, a negligible amount of time (8.6%) was spent in all distance classes greater than 30m. About sixty-two percent of the time was spent in the 0-15 m distance class (Fig. 8b).

The AM in February spent 34.6% of the time within the 0-15 m class, and 34.08% in the 46-60 m distance class. But use intensity decreased as distance increased with the maximum distance moved being 90 m from the nest tree (Fig. 8a). In March, the pattern was similar to that for February for the AM though a greater percentage of time (50.58%) was spent in the 0-15 m class than in February. The distance class 46-60 m was used for 27.89% of the time and the maximum distance moved was 60 m. In April, the AM spent 52.19% of the time in the 0-15 class and 31.14% in the 16-30 m distance class. Maximum distance moved was 75 m.

The SAM showed a similar trend as the other two squirrels, with intensity of use falling as distance from the nest increased. Use in the 46-60 m class was 22.4% in February. In March, there was a similar trend (Fig. 8c). The SAM male showed a different trend in April and this is the only instance when percent time spent in the 0-15 m class was not the highest (30%). It was highest in the 16-30 m class and the maximum distance moved was 135 m (Fig.8c).

4.7 Activity budgets:

The hourly percent activity for each month was calculated for the squirrels in Bhainsa Nala only.

In the winter months (December-February), activity time was distributed throughout the day with a peak from 0830 to 0920 hours (Fig.10). Daylength was around 10 hours in winter. Afternoon activity ranged from 29% to 43% for the squirrels. Squirrels emerged from their nests after daybreak and returned to their nests before the onset of nightfall. In summer the total active time increased with daylength increasing 12 hours 20 minutes in April. Squirrels emerged from their nests half an hour earlier than sunrise in April. In both seasons, squirrels went into their nests either by mid-morning or afternoon to rest. As the days lengthened, activity began earlier and ended by 0900 hrs in April. After an early morning peak, squirrels returned to their nests to rest, before resuming activity later in the day. But in April, two squirrels did not go into their nests at all at mid-day and rested in the middle and lower canopy levels of trees in the riparian area. The secondary active periods started later in the day in summer with activity starting from 1600 to 1800 hrs in March, 1700 to 1800 hrs in April. In winter, since squirrels remained somewhat active throughout the day and afternoon activity started earlier. In summer, squirrels did not return to their nests after the onset of nightfall. They remained resting on the nest tree even till 1930 hrs when I would discontinue observations. Most squirrels showed synchrony in the rest periods and secondary active periods. Percent afternoon activity varied from 11.3% to 28.5%. Activity budgets showed a bimodal pattern in both seasons but the peaks were much less pronounced in winter.

4.7.1 Behaviour during periods of activity:

There was monthly variation in percent time spent feeding calculated as the percent of total active time. The individuals showed variation in monthly time spent feeding. Monthly means of percent time spent feeding for all squirrels varied from 45.21% in February to 22.52% in April. Resting varied from 41% to 56%. The AF spent only 16.01% of her time feeding spending 71.42% of her time resting. All three squirrels showed a marked decline in time spent feeding in April (Table 6). There were individual variations in time spent in various activities. Time spent moving did not vary much between individuals and months. Time spent resting increased in the summer months for all squirrels (9a). Percentages for other activities were not calculated separately. Nest building activity by the AM was observed in March and April on three days. Nest building started in the morning after a short feeding bout on these days and the squirrel remained engaged in this activity for a maximum of 90 minutes on one day.

The two focal animals in Churnagundi nala for whom activity pattern data was gathered for winter showed a striking difference from the time budgets of the squirrels in Bhainsa nala (Fig. 9b).

In January, the male spent 32.93% time feeding and feeding time drastically declined in February to only 7.17% with 78.9% of time spent resting. The female which was followed only in January, also spent only 14.26% of time feeding. Percent time spent moving varied from 9.62% for the male to 11.76% for the female in January. Both the squirrels were observed to be basking on open exposed branches in the morning which was the peak feeding time for the squirrels in Bhainsa nala. This unusual activity pattern was likely to have been related to limited food availability.

CHAPTER 5. DISCUSSION

The Indian giant squirrel (*Ratufa indica*) is a facultative frugivore (Borges 1989) becoming a generalist in times of food shortage when it consumes leaves, bark, flowers and pith. But it should be stressed that they feed on these other items even when fruit is abundant, therefore indicating that they may be necessary for mineral requirements (Borges 1989). Payne (1980) considered both seed dispersers (fruit pulp eaters) and seed destroyers (seed eaters) as frugivores. *Ratufa* spp. are essentially seed destroyers.

5.1 INTER-INDIVIDUAL VARIATION IN FLOWER/FRUIT CROP SIZE AND FLOWERING/FRUITING:

There were pronounced inter-individual variations in fruiting within a species. Though as mentioned before I did not estimate relative fruit crop sizes, there were large variations in the size of fruit crops between individual fruiting trees. Trees with minimal fruits as well as trees with a high fruit crop were recorded as fruiting. This can bring in a bias as in reality, squirrels used only a few fruiting trees. This bias especially occurred for *T. arjuna*. Many fruiting trees show variation in crop size from year to year (McClure 1966; Medway 1970; Ng & Loh 1974).

Many studies have demonstrated the heterogeneity in food resource availability in tropical forests. Fruiting cycles have been found to show periodicity (Medway 1970) with sporadic fruiting cycles. In Churnagundi nala, fruit resource availability was very poor compared to that of Bhainsa nala inspite of the 76.92% similiraity in tree species. The reason for such site variation in fruiting is not clear but it is possible that some *T. arjuna* trees in Churnagundi had already fruited in November and been depleted by squirrels and langurs since I noted some *T. arjuna* which had dried up fruits. The unpredictable fruiting cycles in Old and New Worlds may give rise to lean fruiting periods (Borges 1989).

5.2 DISPERSION OF FLOWERING/FRUITING TREES:

The indices used to measure distribution of fruiting trees indicated a near random distribution, but very few of the fruiting trees were actually used by squirrels. The distribution of fruiting *T. arjuna* was also close to random but in March only two fruiting trees adjacent to each other were used.

5.2.1 Selectivity for individual flowering/fruiting trees:

Squirrels seemed to show selectivity between individual fruiting trees of a species. Squirrels used only a few *T. arjuna* trees for feeding. Selectivity between individuals of a species was also seen for *Bombax ceiba*. The flowers of this species became an important resource for squirrels in Feb-March. Since this species was rare and dispersed (index of resource abundance=1), 3-4 squirrels were seen feeding on one flowering tree. An adjacent tree with less flowers was not used. Later, in April this tree was largely used for feeding on fruits. According to optimal foraging models, a patch will be used for feeding if it yields a higher average intake of food value in terms of energy (Pulliam 1974). Since squirrels made forays on occassions it is reasonable to presume that they knew which were the good quality patches. Pyke *et al.* (1977) have suggested that in many vertebrate species the distribution of resource clumps may be known to residents. Steele & Wiegle (1987) found that sampling was important for locating good patches and a means for continuous assessment of relative change in food availability. Trees with low fruit crops may not be profitable because of increased search time and consequently lower rates of intake.

5.3 FOOD RESOURCE USE:

The resource use by squirrels seemed to be determined by the seasonal availability of resources. Fruit was a major source of food in terms of TSF, It was the first ranked among all food items for all squirrels except for the AF in April. Squirrels fed on alternative items at all times, though the %TSF on leaves and bark decreased in April with the availability of a large number of flowering and fruiting trees. As fruits are poor in protein contents, frugivores are known to consume plant parts other than fruits to substantiate the protein requiremnts (Cooper & Charles-Dominique, 1985). Squirrels did not always consume ripe fruit. The consumption of unripe fruits of *Aegle marmelos, Bridelia retusa* and *Mangifera indica* as well as the unripe pods of *Butea monosperma* was recorded. Holarctic tree squirrels have also been found to eat a wide variety of plant and animal matter (Mollar 1983). Although tree seeds are generally high in digestible energy, other food may be necessary for a nutritionally balanced diet (Havera & Smith, 1979; Moller 1983; Short 1976; Short & Epps 1976; Smith 1968). Giant squirrels were observed to feed on termites by Krishnan (1975) and on coccid bugs and soil by Ramachandran (1988). I observed squirrels licking termite-infested bark and eating soil on 4 occassions. The ability to switch to less profitable resources in terms of nutrients is also an adaptation to the fluctuations in resource availability (Borges 1989).

Borges (1989) found figs to be important resources for giant squirrels in lean periods though they were not available to all squirrels. Resources such as figs are usually provided by a small percent of the plant community during periods of fruit shortage and are termed 'keystone resources' (Terborgh 1983; 1986). In Bhainsa nala, as mentioned earlier there were only two *Ficus* trees one each of *F. religiosa* and *F. glomerata*. The *F. glomerata* tree had unripe fruits and was fed on for very short periods, the sprout leaves of this tree were also consumed. These two fig trees were within the male's territory and all squirrels did not have access to these trees when they fruited. The AM invariably chased away intruders from the *F. religiosa* tree, 4 times on one day and thrice on another day in April. He was also intolerant of intruders on any part of his territory at this time. This may seem contradictory to the earlier statement regarding the tolerance of individuals at a locally abundant food source. But the other resources at which individuals tolerated each other were at the periphery of ranges whereas this fig tree was near to the AM's nest tree. Limited feeding time may have been a crucial factor in excluding other individuals from access to this tree. In April, feeding time was curtailed due to the heat, when the squirrels would start resting or go into their nests by 0900 hrs so the other individuals who were excluded from the fruiting tree would be denied access at an optimal feeding time. Since high ambient temperatures precluded feeding after a certain point, this reduced overall TSF in a day and a squirrel who was denied access would lose out on the resource. For some squirrels it was not just territorialty but the location of the resource which precluded its use. The impact of exclusion from prime resources will be discussed in detail in Section 5.6.

5.4 SELECTION RATIO FOR FLORAL AND FRUIT RESOURCES:

Selection ratios for floral and fruit resources will only be discussed for focal individuals in Bhainsa nala. For the adult male (AM), both the floral resources used; *Bombax ceiba* and *Peltophorum ferruginea* showed low use. The low preference for *Bombax ceiba* in February could be due to the fact that the sprouting buds had just become available and were scarce. Squirrels were also observed to inspect, search for and reject buds and since buds were scarce, squirrels did not spend a long time feeding on *Bombax ceiba* in February. The same trend was seen for the SAM. With the availability of mature flowers in March, the selection ratios indicated a high preference for both squirrels. *T. arjuna* fruits showed medium to low preference inspite of it being the first ranked resource in terms of TSF for AF and SAM in February and March. This is due to the disproportionately high availability of fruiting *T. arjuna* relative to other species. The high preference for *Bridelia retusa* by AM in February is indicative of the importance of this resource which is relatively rare. All individuals had a low preference for flowers of all species except *Bombax ceiba* and *Careya arborea* but since nutritional analysis was not carried out it is not possible to explain the differential preferences for food species.

The semi-ripe fruits of *Aegle marmelos* and the fruits of *Bombax ceiba* were highly preferred by AF. In April, AF showed a very low preference for the two fruit species (*Mangifera indica* and *Butea monosperma*) in her diet. This is possibly due to the fact that these species had unripe fruits which were not preferred. This may be related to the low sugar content. Unripe fruits which had a low sugar content (<13%) were not preferred by flying foxes (S.P. Goyal, *pers. comm.*). The fruits of *F. religiosa* were a highly preferred resource for the adult male in April. Earlier in March when the tree had unripe fruits it had a low preference. The very high preference value (28.84) is likely to be due to the extremely low availability. The sub-adult had a high preference for *Bombax ceiba* fruits. Thus squirrels seemed to show selectivity for floral and fruit resources depending on their phenophase which determines palatability of a resource.

The variability between the individuals in the use of different item classes and even of food species is evident (Table 2a, 3a-3c). For instance when AM spent 70.09% of time feeding on the ripe fruits of *Ficus religiosa*, the AF spent the maximum time feeding on flowers mainly of *Careya arborea*. The monthly variation among individual squirrels both in terms of food species utilized as well as %TSF on different food items shows that some squirrels included lean season foods in their diet while others were eating fruit. Squirrels did not experience fruit shortages in their range simultaeneously. This is because of the distribution and density of certain food species which may not have been accessible to all squirrels. Since the three squirrels were observed at nearly the same time of the month, change in phenology between observation days can be discarded as being the cause for this variation in use. The variation in food species use observed between squirrels is due to the restricted access to food species for some individuals either due to exclusion from a resource by a conspecific or due to the distribution and location of resources far away from the range of the individual (Borges 1989).

5.5 RESOURCE ABUNDANCE AND USE:

I tested the hypothesis that squirrels use resources as they are encountered in the habitat using Pearson's correlation (   ). If this occurred there should have been a positive correlation between resource abundance and resource use. The other alternative is that squirrels search for specific resources which may not necessarily be abundant. When the indices of resource abundance for each species were compared to their percentage use, no significant correlation was found (Fig.15). This indicates that squirrels searched for specific resources and the high abundance of a species did not necessarily mean high use. This also implies that relatively rarer species in habitats are vital food sources for the squirrels. *T. arjuna* was the only positively correlated resource.

5.6 TERRITORIALITY AS A FACTOR AFFECTING SPACE-USE PATTERNS:

The timing of visits can be a critical aspect of the use of space. This is of considerable importance for animals with overlapping territories (Getty 1981b). Territorial aggression is well known in chipmunks and is spatially organized (Burt 1940; Dunford 1970; Elliott 1978). Getty (1981a) has suggested that within crowded chipmunk groups, neighbours may interfere with the timing of movements but not the total quantity of access to space. He found that although neighbours fight when they meet, home ranges overlap without exclusive core areas. Borges (1989) suggested that neighbouring squirrels would employ avoidance tactics using spatial time sharing. This could have been achieved by scent-marking and vocalizations.

I recorded vocalizations related to territorial advertisement a number of times, but I rarely observed scent-marking. I cannot discount the fact that I may have missed some instances of scent-marking. But on the occassions on which it was observed it usually occurred as the squirrel left a food tree after a feeding bout or after an aggressive interaction. I recorded vocalizations where a neighbouring female would resort to territorial advertisement. Borges (1989) has described this as a loud staccato call becoming softer and my observations regarding these vocalizations support her description. Squirrels may engage in such vocalization for upto 15 minutes. Neighbouring individuals would also engage in this call. Most squirrels also would utter this call within their nests before leaving the nest and on coming out of the nest.

The feeding aggregations observed on certain flowering or fruiting trees were due to the local abundance of resources. There was overlap in time and space and though squirrels tolerated each other's presence, aggressive interactions occurred at these common food sources whenever two feeding individuals came within 5-6 m of each other. Inter-individual distance maintenance may be a mechanism by which squirrels avoid each other when overlap in time and space occurs. I believe that when food resources are locally abundant they are commonly used by most individuals with no one individual being the sole territory owner. Wroughton (1915) has even described this race *centralis* as gregarious since he also observed feeding aggregations on one food tree.

Another factor which may have resulted in tolerance of individuals is the fact that it may be unprofitable and impossible for any one squirrel to defend a resource against many individuals especially when the resource is locally abundant. The costs of energy expenditure and loss of feeding time due to defence of the resource may outweigh the benefits resulting from exclusive rights to a resource (Brown 1964). Time spent in aggression is time lost in feeding.

Many aggressive interactions were inconclusive in the sense that the recipient remained on a food tree and the aggressor seemed to tolerate its presence after establishing dominance. At times, after an aggressive interaction occurred the recipient would return to the food tree after the aggressor left. One possible explanation of tolerance of conspecifics at food sources could be that there is already an established dominance hierarchy in which known neighbours are tolerated. Familiarity can decrease the absolute numbers of aggressive interactions between individuals (Armitage 1977). Older animals have been found to be dominant in some marmot species (Armitage 1975; Dunford 1977) leading to avoidance behaviour by subordinates and possibly to a decrease in absolute levels of interaction rates. Since the relationships among individuals are not known, it is not possible to say whether the individuals who tolerated each other at food trees were related. It must be stressed that though tolerance was seen at times among feeding individuals, aggressive interactions were common; resulting in the exclusion of some squirrels from food sources. Thus the presence of neighbours and consequently territorialty affected the space use patterns of individual squirrels. In one instance, a squirrel was chased away from the flowering *Bombax ceiba* which at the time had a low abundance of sprouting buds, the dominant individual who had access first depleted most of the buds. When the subdominant later returned to the tree it had access to very few buds. Thus though exclusion from a food source may not be total it seems to reduce access and also may affect the time budget of the animal. Since neighbours seemed to interfere with each other's use pattern, intraspecific competition is likely.

During the study, a focal male with a cut ear was observed for two days in December. His range overlapped with the AF's and he was frequently chased by all individuals he came into contact with. He was displaced from his nest tree while nest building on the approach of the AF. Such aggressions often occur and are counter to the usual predictions, indicating the existence of other factors affecting social interactions. Individual differences in psychological makeup and physical prowess (size and strength) exist and these affect the results of aggressive encounters (Elliott 1978). These differences may be viewed as independent of space in that they remain constant regardless of spatial location of individuals (Elliott 1978). Experiments by Wolfe (1966) and by Ickes (1974) on captive chipmunks, where all individuals were equally familiar with neutral areas, found that a hierarchy based on space-independent elements of dominance such as fighting ability correlated with size. Wolfe (1966) felt size was the critical factor influencing position in the hierarchy. Some observations of Elliott (1978) also suggested such factors to be true in wild squirrels. He suggested that learned relationships between specific individuals are important in the formation of dominance hierarchies especially if they lead to decrease in overt aggression and result in establishment of dominance-subordinance relationships. Usually the individual's likelihood of dominance in aggressive social encounters is greatest near its nest tree. But site-independent individual differences in physical attributes or psychological makeup may also exist in nature (Elliott 1978) as shown by these observations. The SAM also showed dominance only near his nest tree and in other areas was usually the recipient of aggression.

The individual with the cut ear (CEM) could not be located later in February. Later, I observed another male using this individual's nest so I believe that it could have been an instance of territory displacement, though predation cannot be discounted as the reason for his disappearance. The male could have been trying to establish a territory since he moved over a large area and used two nests far away from the usual nest tree on two occassions. Borges (1989) observed a case of an attempted territory take-over where the individual finally left presumably to establish territory elsewhere. Borges (1989) has suggested that such 'floaters' would be severely handicapped not only with respect to access to food sources but also with regard to access to females.

Studies on the American Red squirrel (*Tamiasciurus hudsonicus*) have shown that they are strictly territorial (Smith 1968; Rusch & Reeder 1970) whereas *Sciurus* spp. have overlapping ranges. Such a difference in social systems has been attributed to the different habitats they use (Don 1983). Easily defended resources are predictable in time and space. *Tamiasciurus* defend stored cone supplies (Gurnell 1984). Benson (1980) has suggested that a possible reason for the lack of a strict territorial system in *Sciurus* is due to the fact it mainly inhabits deciduous forests where deciduous trees are so heterogenous in their temporal and spatial distribution that a single exclusive area guaranteed of sufficient food would be too large to defend, hence *Sciurus* spp. have overlapping and temporally dynamic ranges are found. *Ratufa indica* is also an animal of deciduous forests, though in some parts of its range it inhabits tropical rain forests. *Ratufa* spp. do not store food (Payne 1980; Borges 1989; this study). The size of ranges and unpredictability of resources precludes the defence of an exclusive area. Thus the territorial system of *Ratufa* is complex with overlapping ranges in which overt aggresion occurs as well as encounter avoidance by spatial time sharing.

5.7 USE INTENSITY OF AN AREA IN RELATION TO DISTANCE FROM DREY:

The establishment of a cache or a nest imposes a quality of distance on the surrounding area (Getty 1981b). Home range use intensity patterns are highly irregular and vary considerably from individual to individual. Though usually the highest intensity of use was within 15m from the nest tree, the high use of some distance classes further from the nest is because these were used for foraging. Unlike temperate squirrels which tend to return to the central place frequently during foraging bouts to feed on a central perch (Getty 1981b), the giant squirrels' movements are directed towards food sources, but after the morning's feeding bouts, all the squirrels would return to their nest tree to rest for some time on the nest tree or re-enter the nest tree in the afternoon. This pattern was especially evident in summer months when the temperatures were high. The squirrels would confine their activities within 15m of the nest tree for a greater part of the day, moving to adjacent trees to feed for some time returning frequently to their nest tree to rest. The AF reduced her movements in April feeding on the bark and leaves of the nest tree itself. In some instances nest trees would be located close to a food source or be a food source itself as in the case of the AF in December and the AM in April. Her movements were therefore confined to two to three other trees near the nest tree which had a large fruit crop.

In April, the AF did not move much, (due to the presence of the pup which followed her to nearby trees imitating the mother's feeding actions). As suggested earlier, feeding time in summer was limited. This may be the reason why she confined her feeding activities to her territory and tried to maximize feeding there. The duration of aggression was also the least in April (Section 4.6) and this is likely to be due to the fact that the AM and AF remained confined to their own territories. The AM because he had adequate resources within 30 m from his nest tree. The AF's movement may have been restricted due to the presence of the pup who followed the mother to nearby trees within 20 m from the nest tree but did not accompany her on longer foraging trips. She therefore confined her activities to within 50m from the nest grid. In December, her range was also small (Table 7). and this was due to the presence of two fruiting trees of *T. arjuna* with a large fruit crop with one being the nest tree itself and the other one within 15m. The maximum distance she travelled for foraging was upto 50m to a fruiting *T. bellerica*. The AF was possibly pregnant at the time, she spent long hours in the nest at daytime. But in February, the fruit crop in these trees declined and she made a long linear movement in search of food. The additional nutrients and energy required due to lactation may have necessitated the consumption of energy rich resources and since the pup was at the time still confined to the nest, her movements were not restricted. Lactation has been found to increase the energy and nutrient requirements of rats (Nelson & Evans 1961) and the white-footed mouse (*Peromyscus leucopus*) (Millar 1975). By March, the fruits of *T. arjuna* were completely depleted near her nest tree and she made foraging trips to feed on a fruiting *Aegle marmelos* with semi-ripe fruits. In March though the pup had emerged out of the nest it remained confined to the nest tree and still spent long hours in the nest so the female's movements were not restricted. The pup had still not been weaned and the AF's energy demands must have been high. The AF spent the highest percentage of the time feeding on bark. This is possibly due to either of two reasons which may seem contradictory a) the relative non-availability of alternative resources within her range but as has been stated before all squirrels were observed feeding on bark even when fruit was available indicating that bark is an essential requirement for other reasons. b) Bark feeding could have been higher for the female because of her increased demands for minerals while lactating. The calcium demands for a lactating female are high as compared to that of a male (Nelson & Evans 1961) and bark is rich in calcium content (Borges 1989). Squirrels at times made long forays out of their usual range without feeding. These movements could be related to information gathering regarding the state of resource availability in the habitat.

5.8 HOME AREA SIZES AND OVERLAP:

Range sizes of *Ratufa bicolor* and *R. affinis* were found to be 9 ha in the tropical rainforest of Malaysia (Payne 1980). Home range size for the smaller-sized *Ratufa macroura* was determined to be 0.82 ha (Joshua 1991). Borges (1989) found an average range size of 1.2 ha for males and 1.1 ha for females at Magod and 0.7 ha for males and females of *Ratufa indica* at Bhimashankar.

The overall range sizes for the three squirrels did not vary much. The male showed overlap with the female's range in winter. This was the mating season and the male was frequently seen in the female's range , following the female. Male chipmunks have been found to invade the home range centres of females making directed approaches towards the resident females. The female chipmunks chase away males when not in breeding condition. Some males are persistent, tolerating several chases in succession before leaving the female's area (Elliott 1978). This kind of behaviour by several males was seen during the study period in winter. But I believe the mating season starts earlier in November-December, since pups were seen towards the end of February when they emerged from the nursery nest. The gestation period of *R. indica* is around five weeks. Pups emerge from the nest after a month being weaned after approximately 5 months (Borges 1989). Besides the focal AF, two other females were also seen with pups at the end of February.

No overlap between the home areas of the AM and AF occurred in summer when locations were considered. But if daily movements (from continuous focal data) over grids are considered, the AF made forays into the AM's range in summer. These movements might have been exploratory to assess resource availability. The AM and SAM's home areas overlapped in both seasons. Summer home area was smaller for the AM since no trips in search of oestrous females were made and food was available near his nest tree. This is also supported when monthly ranges in terms of quadrats used are considered (Table7) when the AM had a larger range size in February while range size was smaller in March and April when resources were available near the nest tree. For the AF, summer range was larger since she made long foraging trips but in reality this was confined to March. In April her activities were concentrated around her nest grid. This trend is also supported when monthly range size in terms of grids used are taken (Table7). The SAM's range was also larger in summer due to long forays which did not necessarily result in feeding. As mentioned before there were other squirrels in the area whose range overlapped with those of my focal animals. Therefore a complete picture of the organization of ranges is missing.

The total home areas calculated from focal data are dependent on observation time. Increased observation time leads to an expansion of the estimated home range limits (Elliot 1978). Further, each squirrel was followed for only two days a month. Thus a time-area curve is invaluable in determining the adequacy of home range estimates. The cumulative number of quadrats seemed to stabilize for all focal animals and varied from 2 days for the AM to 5 days for SAM. The SAM as stated earlier had a range overlapping another female's. Interactions between them have been described earlier in Section 4.5. It is possible that he is a previous year's pup and is yet to establish a territory and therefore moved more than the other two focal animals.

5.9 FACTORS INFLUENCING ACTIVITY PATTERN:

Besides the endogenous rhythm of activity patterns, a number of external factors such as variation in daylength, food supply, temperature may affect activity patterns (Tonkin 1983).

5.9.1 Influence of food supply on activity pattern:

The resource shortage in the squirrels' ranges in Churnagundi had a marked effect on their activity patterns. The unusual activity pattern of the two squirrels is likely to be related to food availability. An animal facing severe food shortages can undertake a number of strategies which could be a) Move over larger areas in search of food b) feed on alternative food items c) emigrate to better areas d) conserve energy by basking (Borges 1989). The squirrels here resorted to a combination of the first and last strategies. Both the male (BEM) and the female (CTF) made some forays presumably to search for food. This is evidenced by the larger range size of the BEM (Section 5.8) compared to those of squirrels in Bhainsa nala. But these movements were of short duration and both squirrels returned to their nest trees to rest or rested in the top or middle canopy for a large part of the day. The male's total feeding time was only 17 minutes during an observation day when he consumed bark. He spent two hours in the nest in the morning and again re-entered the nest in the afternoon. He did not come out of the nest till 1700 hrs when I discontinued observation. Fig. 3a & 3b show the percent time spent

on different activites by these squirrels in winter. This unusual activity pattern is unlikely to be related to thermoregulation due to a number of reasons. Firstly, temperatures were colder in January than in February (Table 1) so if the prolonged periods of resting were due to the cold, the male should have shown this behaviour in January too. But in January he spent 49.66% of the time resting in contrast to 78.9% of the time resting in February. In January, he still had fruit resources in his range (Section 4.3). Secondly, at the time when the two squirrels were basking or resting, the focal squirrels in Bhainsa nala would be feeding. Their major feeding period was from 0700 - 1100 hrs in winter. If the long periods spent basking in winter were due to cold stress, it should have been true for Bhainsa nala squirrels too. The squirrels in Bhainsa nala were rarely observed basking for periods greater than 15 minutes in the morning. The squirrels in Churnagundi would bask on exposed branches. This strategy could have been employed to conserve body heat. When food availability is low it may be adaptive to conserve energy so that minimum calories are required for maintenance (Hudson & Broadley 1972). Though of the total TSF, the greatest %TSF was on bark, the squirrels spent a lesser total time feeding on these items compared to Bhainsa nala squirrels which also had access to fruit resources. This could be due to the fact that bark is fed on as a supplement being fed on only for mineral requirements and not as an energy source (Borges 1989). Also the processing and handling times required to feed on bark may cost more in terms of energy than any benefits obtained from feeding on it for a longer duration (Ajith Kumar *pers. comm.*). The large size of *Ratufa* may ensure its survival even during periods of food shortage by its capacity to fast (Borges 1989). Since fasting endurance has been found to scale allometrically with body size (Lindstedt & Boyce 1985) restricted feeding can be endured.

5.9.2 Influence of temperature and daylength on activity pattern:

One of the striking features of the time budgets of squirrels in Bhainsa nala is that a large percentage of the diurnal active time is spent resting. Borges (1989) suggested that this could be because it needs time to digest gut contents and to avoid heat or cold stress. It is unlikely that squirrels experienced cold stress in the study area since they were observed feeding even at a temperatures of 6^0C. The lowest temperature was recorded in December (5^0C). The decline in time spent feeding is especially marked in April when squirrels would become active before dawn and retire into the nest or rest by 0900 hrs. The secondary active period would only start after 1700 hrs and squirrels would return to their nests around 1930 hrs. In this way they tried to compensate for the restricted feeding time during the day. Squirrels have been found to become inactive out of the nest at high temperatures contributing to the lull in activity during mid-day in summer (Gurnell 1987). Squirrels were seen to adopt spreadeagled heat dispersing postures as described elsewhere (Purroy & Rey 1974; Shorten 1962; Borges 1989). The bimodality in activity patterns was more pronounced in summer. This was due to the high temperatures which resulted in squirrels being inactive for a greater part of the day from around 0900 to 1630 hrs. In winter, squirrels remained somewhat active throughout the day since temperatures were more equable. The onset of activity shifted from 7 hrs in winter to 530 hrs in summer and cessation of activity from 1730 hrs in winter to 1930 hrs in summer. *Ratufa indica* has been also found to be bimodal in both seasons by (Borges 1989) but *Ratufa* spp. in the rain forests have been reported to show no bimodality in activity patterns and also to begin activity earlier and end activity later than other diurnal frugivores (Payne 1980). Tropical rainforests have more stable climates with no extreme variations. The mean maximum temperature does not rise beyond 36°C (Puri *et al*. 1972) In the study area, temperatures rose to 42-43° in April. Other factors which could affect activity pattern are individual variation related to age or breeding condition (such as lactating females)). The AF greatly reduced her activity when she was pregnant in December spending 51.19% of the day resting in the nest. The SAM remained active for longer periods than the other focal animals exiting the nest earlier and returning later to the nest in the evenings. The SAM continued its feeding activity even after other squirrels had re-entered their nest. This could be related to avoiding competition with adult squirrels.

One striking feature observed in the study is the tendency of most squirrels to retire to their nests at daytime both in winter and summer irrespectve of age or sex class. Squirrels have been observed to use nest in daytime (Joshua 1992; Borges 1989) but not for such long durations. Though Gurnell (1987) describes that in summer squirrels rest outside the nest since inside the nest it may be hotter due to insulation, it is likely that nests have a more stable environment than the outside. Further, squirrels rarely slept when resting outside (mostly eyes were kept open). The need to stay alert when resting outside due to the presence of aerial predators (seen active in the afternoons) such as Crested hawk eagle and Crested serpent eagle, could be the reason for sleeping in the nest. Though the evidence is anecdotal, I observed an unsuccessful predation attempt by an immature Crested Hawk eagle on the SAM which was resting outside in the afternoon. The SAM was in a semi-alert state when the predator attacked. Squirrels which remain resting outside could be more vulnerable to predation in their semi-alert state.

Human disturbance in the form of noise, constant human activity and the presence of a diesel pump in Bhainsa nala did not affect the squirrels' activity pattern since they continued to feed near such sources of disturbance. The AM used a nest on a tree 10 m from the diesel pump. But squirrels were forced to travel on the ground at least 3-4 times a day due to canopy gaps in many places travelling upto 20 m on the ground. Squirrels were never observed to travel on the ground in Churnagundi. The squirrels in Bhainsa nala were habituated to human presence and there was hardly any effect on behaviour due to disturbance. But the canopy gaps and the large patch of forest cleared along one side of the nala for 1.5 km have reduced the habitat available for squirrels but inspite of this in the intensive study area of 9.48 ha at least 6 individuals were known.

5.10 CONCLUSIONS:

1. There was variation in the food species as well as the food items used by individual squirrels.
2. The variation in the use of food items and species was due to resources not being accessible to all squirrels.
3. Squirrels consumed lean season foods such as bark and leaves even when fruit and flowers were available suggesting that these food items were necessary for other nutritional requirements.
4. Squirrels selectively utilized certain individuals of a fruiting or flowering tree in relation to the fruit crop size.
5. The selective utilization of a few fruiting or flowering individuals resulted in overlap in time and space at these locally abundant resources. Squirrels tolerated each other's presence at these resources by maintaining individual distances.
6. Squirrels formed specific search images while foraging and did not utilize resources as they were encountered. Thus the rarer species in the habitat were relatively important components of squirrel diet.
7. The variation in resource use between individuals is due to the restricted access to food species for some individuals either due to exclusion from a resource by conspecifics or due to the distribution and location of resources far away from the range of the individual.
8. Feeding time was greatly curtailed in summer due to the high temperatures therefore squirrels who were denied access to

resources at an optimal feeding time would lose out on a resource since feeding after a certain point was not possible.

9. The temporal and spatial heterogeneity of resources in deciduous habitats precludes the defence of an exclusive area of the day resting and remained confined to their nest trees.

10. Limited food availability affected the activity budgets of squirrels in one area, when they adopted a strategy of conserving energy by resting for long durations.

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APPENDIX I. List of recorded behaviours include:

1. Feeding:
   - Searching
   - Inpecting food items
   - Ingesting
   - Breaking (twigs)
   - Stripping (bark)

2. Resting:
   - resting horizontally
   - resting vertically
   - resting with fore and hind limbs outstretched and flattened
   - basking (when exposed to sun)

3. Vocalizations:
   - Alarm calling
   - Clicking call
   - Communicatory call (2 types)

4. Grooming:
   - Autogrooming
   - Scratching
   - Rubbing

5. Social interactions:
   - Allogrooming
   - Mother-pup interactions
   - Pursuit (by male)

6. Others:
   - Nest building
   - Nest repairing
   - Nest inspection
   - Drinking (licking dew from leaves and water from tree hollows)
   - Urinating
   - Defecating
   - Scent-marking
   - Playing
   - Chasing

7. Anti-predatory behaviour:
   - Alert posture
   - Mobbing of predator
   - Freezing

8. Aggression (chase)

9. Movement:
   - Moving within tree
   - Moving between trees
   - Moving on ground

APPENDIX IIa Relative abundance of tree species in Bhainsa Nala.

(total area covered by grids = 4.29 ha)
(no. of grids = 189)

SPECIES	RELATIVE ABUNDANCE OF EACH SPECIES (%)
1. *Butea monosperma	15.75
2. *Terminalia arjuna	13.00
3. Saccopetalum tomentosum	12.00
4. *Syzygium cumini	11.00
5. Tectona grandis	7.32
6. *Madhuca indica	5.20
7. *Terminalia tomentosa	4.70
8. *Aegle marmelos	4.50
9. Diospyros melanoxylon	4.50
10. *Mangifera indica	2.85
11. *Careya arborea	2.60
12. *Terminalia bellerica	2.35
13. *Phyllanthus emblica	2.20
14. Pongamia pinnata	1.98
15. Anogeissus latifolia	1.98
16. *Peltophorum ferruginea	1.30
17. *Lagerstromia parviflora	1.30
18. Zizyphus xylopyra	1.20
19. *Acacia auriculiformes	0.98
20. *Bombax ceiba	0.98
21. *Buchnania lanzan	0.98
22. Bauhinia variegata	0.62
23. Delonix regia	0.86
24. Lannea coromandelica	0.37
25. Grewia tiliaefolia	0.37
26. *Tamarindus indica	0.37
27. Trema orientalis	0.37
28. Scliechera oleosa	0.37
29. Albizzia lebbeck	0.24
30. Mallotus philippinensis	0.24
31. *Ougeinia ougeinensis	0.24
32. Mitragyna parviflora	0.24
33. Acacia leucophloea	0.12
34. *Ficus religiosa	0.12
35. *Ficus glomerata	0.12
36. Sterculia urens	0.12
37. Casearia graveolens	0.12
38. Stereospermum svaveolens	0.12
39. Dalbergia paniculata	0.12
40. Flacourtia indica	0.12
41. *Zizyphus rugosa	0.12
42. Unknown species	0.12

* Recorded food species

APPENDIX IIb Relative abundance of tree species in Churnagundi Nala. (total area covered by grids = 1.89 ha) (no.of grids = 84)

SPECIES	RELATIVE ABUNDANCE OF EACH SPECIES (%)
1. **Madhuca indica*	12.20
2. *Diospyros melanoxylon*	10.45
3. **Terminalia arjuna*	9.80
4. *Saccopetalum tomentosum*	8.06
5. **Phyllanthus emblica*	6.97
6. *Lagerstroemia parviflora*	5.88
7. **Terminalia bellerica*	4.35
8. *Careya arborea*	3.48
9. *Grewia tiliaefolia*	2.83
10. *Scleichera oleosa*	2.61
11. *Chloroxylon indica*	2.61
12. *Terminalia tomentosa*	2.39
13. *Aegle marmelos*	2.39
14. *Lannea coromandelica*	2.17
15. *Zizyphus xylopyra*	1.96
16. *Buchnania lanzan*	1.52
17. *Butea monosperma*	1.52
18. *Mitragyna parviflora*	0.87
19. *Anogeissus latifolia*	0.87
20. *Mangifera indica*	0.65
21. *Albizzia lebbeck*	0.65
22. *Adina cordifolia*	0.43
23. **Semecarpus anacardium*	0.43
24. *Kydia calycina*	0.43
25. **Bridelia retusa*	0.43
26. **Ficus benghalensis*	0.21
27. *Bombax ceiba*	0.21
28. *Stereospermum svaveolens*	0.21
29. *Sterculia urens*	0.21
30. *Acacia leucophloea*	0.21
31. *Terminalia chebula*	0.21
32. *Ougeinia ougeinensis*	0.21
33. **Tamarindus indica*	0.21
34. Unknown species	0.21
35. Unknown species	0.21

* Recorded food species (only in winter)

Table 1: Monthly mean temperatures recorded during the study period.

MONTH	MEAN MINIMUM (^{0}C)	RANGE (^{0}C)	MEAN MAXIMUM (^{0}C)	RANGE (^{0}C)
DECEMBER	8.1	8.0-8.5	27.0	27.0-27.0
JANUARY	9.4	6.0-12.0	27.6	26.0-29.0
FEBRUARY	9.1	6.5-16.0	29.9	26.0-33.0
MARCH	13.0	11.5-16.0	33.3	23.0-37.0
APRIL	18.8	15.5-21.0	42.0	34.0-43.0

Table 2a: Monthly means of percent time spent feeding on different food items for individual squirrels.

	MONTH	FRUIT	FLOWER	LEAF	BARK
AM	Feb.	80.30	6.27	2.35	11.05
AF	Feb.	56.70	19.73	2.53	21.00
SAM	Feb.	65.94	19.63	7.57	6.80
AM	Mar.	61.74	16.48	3.5	18.21
AF	Mar.	61.18	8.43	2.4	27.96
SAM	Mar.	56.76	21.50	3.64	17.71
AM	Apr.	79.02	17.42	3.06	1.37
AF	Apr.	5.32	62.26	23.14	8.38
SAM	Apr.	53.60	39.80	2.00	3.00

AM = adult male ; AF = adult female ; SAM = subadult male.

Table 2b: Monthly means of percent time spent feeding on food item classes for all three squirrels.

MONTH	FRUIT	FLOWER	LEAF	BARK
Feb.	67.80	15.30	4.20	12.10
Mar.	59.88	15.72	3.16	21.19
Apr.	45.96	39.82	9.59	4.17

Table 3a: Monthly selection ratio (SR) and percent availability (%A) for floral and fruit resources for the adult male.

SPECIES	FOOD ITEM	% A	FEB. SR	% A	MAR. SR	% A	APR. AR
Bombax ceiba	flower	30.92	0.07	6.15	2.58	0	-
Peltophorum ferruginea	flower	53.84	0.04	0	-	0	-
Madhuca indica	flower	0	-	16.92	0.03	13.00	0.18
Bridelia retusa	fruit	10.00	2.51	15.78	0.61	0	-
Terminalia arjuna	fruit	66.66	0.74	42.1	1.19	0	-
Ficus glomerata	fruit	3.3	0.80	0	-	0	-
Ficus religiosa	fruit	0	-	2.43	0.65	2.43	28.84
Butea monosperma	flower	0	-	0	-	30.89	0.27
Syzygium cumini	flower	0	-	0	-	39.02	0.06
Zizyphus rugosa	flower	0	-	0	-	0.81	4.91
Mangifera indica	fruit	0	-	0	-	9.75	0.91

Table 3b: Monthly selection ratios (SR) and percent availability (%A) of fruit and floral resources for the adult female.

SPECIES	FOOD ITEM	FEBRUARY		MARCH		APRIL	
		% A	SR	% A	SR	% A	SR
Buchnania lanzan	flower	15.38	0.17	-	-	-	-
Peltophorum ferruginea	flower	53.84	0.32	10.76	0.04	4.06	0.50
Terminalia arjuna	fruit	66.66	0.66	40.00	0.07	-	-
Terminalia bellerica	fruit	3.33	2.02	-	-	-	-
Aegle marmelos	fruit	3.33	1.0	15.00	3.17	-	-
Phyllanthus emblica	fruit	13.33	0.10	-	-	-	-
Butea monosperma	flower	-	-	21.53	0.11	30.89	0.01
Madhuca indica	flower	-	-	16.92	0.01	13.00	0.91
Bombax ceiba	flower	-	-	6.15	0.85	-	-
Bombax ceiba	fruit	-	-	5.00	1.6	-	-
Ficus glomerata	fruit	-	-	5.00	0.17	-	-
Ficus religiosa	fruit	-	-	5.00	0.26	-	-
Careya arborea	flower	-	-	-	-	8.13	4.4
Syzygium cumini	flower	-	-	-	-	39.02	0.21
Zizyphus rugosa	flower	-	-	-	-	0.81	3.5
Butea monosperma	fruit	-	-	-	-	75.6	0.04
Mangifera indica	fruit	-	-	-	-	9.75	0.20

Table 3c: Monthly selection ratio (SR) and percent availability (%A)for floral and fruit resources for the subadult male.

SPECIES	FOOD ITEM	FEBRUARY		MARCH		APRIL	
		% A	SR	% A	SR	% A	SR
Bombax ceiba	flower	30.96	0.63	6.15	2.32	0	-
Madhuca indica	flower	0	-	16.15	0.12	13.00	0.89
Butea monosperma	flower	0	-	21.53	0.23	0	-
Careya arborea	flower	0	-	0	-	8.13	3.46
Bridelia retusa	fruit	10.00	0.24	0	-	0	-
Aegle marmelos	fruit	3.33	0.37	15.78	0.04	0	-
Terminalia arjuna	fruit	66.66	0.91	42.10	1.20	0	-
Lagerstroemia parviflora	fruit	0	-	5.26	0.45	0	-
Bombax ceiba	fruit	0	-	0	-	9.75	4.99
Butea monosperma	fruit	0	-	0	-	75.6	0.06

Table 4: Percent time spent feeding (% TSF) on the top ten food species in both seasons.

WINTER	% TSF	SUMMER	% TSF
Terminalia arjuna	62.07	*Terminalia arjuna*	38.37
Terminalia bellerica	8.50	*Ficus religiosa*	11.92
Bombax ceiba	7.8	*Bombax ceiba*	10.81
Madhuca indica	6.38	*Aegle marmelos*	9.70
Bridelia retusa	4.52	*Madhuca indica*	9.48
Peltophorum ferruginea	3.26	*Careya arborea*	4.4
Tamarindus indica	2.17	*Butea monosperma*	3.9
Ficus glomerata	1.43	*Bridelia retusa*	2.69
Aegle marmalos	0.83	*Mangifera indica*	2.05
Mangifera indica	0.62	*Terminalia bellerica*	1.45

Table 5a: Duration of aggression per day in seconds

Season	All aggression	Feeding aggression	Fruit feeding aggression	Other aggression
Winter	128.84	39.23	78.84	10.76
Summer	129.5	16.33	47.16	63.08

Table 5b: Frequency of aggressive interactions per day

Season	All aggression	Feeding aggression	Fruit feeding aggression	Other aggression
Winter	1.46	0.30	1.00	0.15
Summer	2.08	0.16	0.75	1.16

Table 6: Activity budgets (% of diurnal activity time from nest exit at dawn to nest return at dusk) for focal individuals in Bhainsa Nala.

		Fd	Rst	Mv	Oth
Adult female	Dec	35.68	51.19	6.46	6.64
	Feb	42.01	44.22	8.71	5.03
	Mar	32.73	48.97	12.36	5.91
	Apr	16.01	71.42	6.94	5.60
Adult male	Feb	38.86	45.81	10.55	4.74
	Mar	41.72	42.79	5.27	11.53
	Apr	24.74	56.78	5.93	12.53
Subadult male	Feb	54.80	35.78	7.45	1.93
	Mar	47.20	38.03	9.45	5.98
	Apr	26.81	39.85	14.97	18.35

Table 7: Monthly ranges of focal squirrels in hectares (ha) in terms of grids used.

	MONTHLY RANGES(ha)			
	FEBRUARY	MARCH	APRIL	OVERALL
ADULT MALE	1.05	0.60	0.51	0.72
ADULT FEMALE	0.90	1.35	0.58	0.94
SUB-ADULT MALE	0.69	0.99	1.01	0.89

Table 8: Index of resource abundance and percent time spent feeding (% TSF) on each floral and fruit resource.

SPECIES	INDEX OF RA	% USE (TSF)
FRUIT RESOURCES		
Terminalia bellerica	5	0.8
Aegle marmelos	15	5.91
Bombax ceiba	1	6.32
Terminalia arjuna	28	29.36
Ficus religiosa	1.5	8.11
Ficus glomerata	2.5	0.66
Butea monosperma	8	0.90
Bridelia retusa	2.5	4.15
Mangifera indica	5	1.22
Lagerstroemia parviflora	2	0.26
FLORAL RESOURCES		
Peltophorum ferruginea	15	2.56
Bombax ceiba	3	6.4
Careya arborea	4	7.19
Madhuca indica	10	3.21
Butea monosperma	10	1.84
Syzigium cumini	16	1
Buchnania lanzan	2	0.3
Mangifera indica	10	0
Acacia auriculiformes	3	0.13
Zizyphus rugosa	1	0.76

FIG I. MAP AND LOCATION OF BORI WILDLIFE SANCTUARY

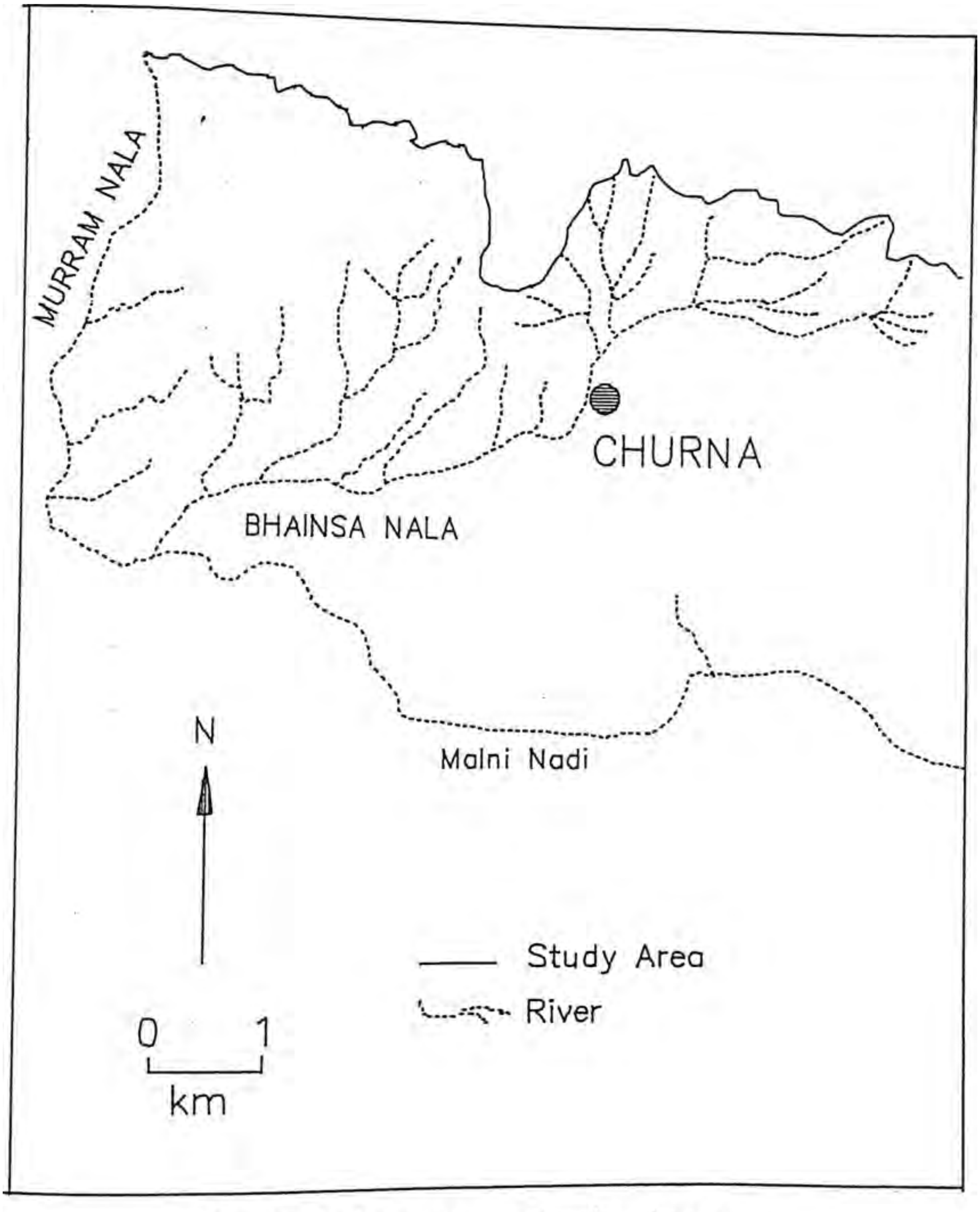


Fig.2 Intensive study area

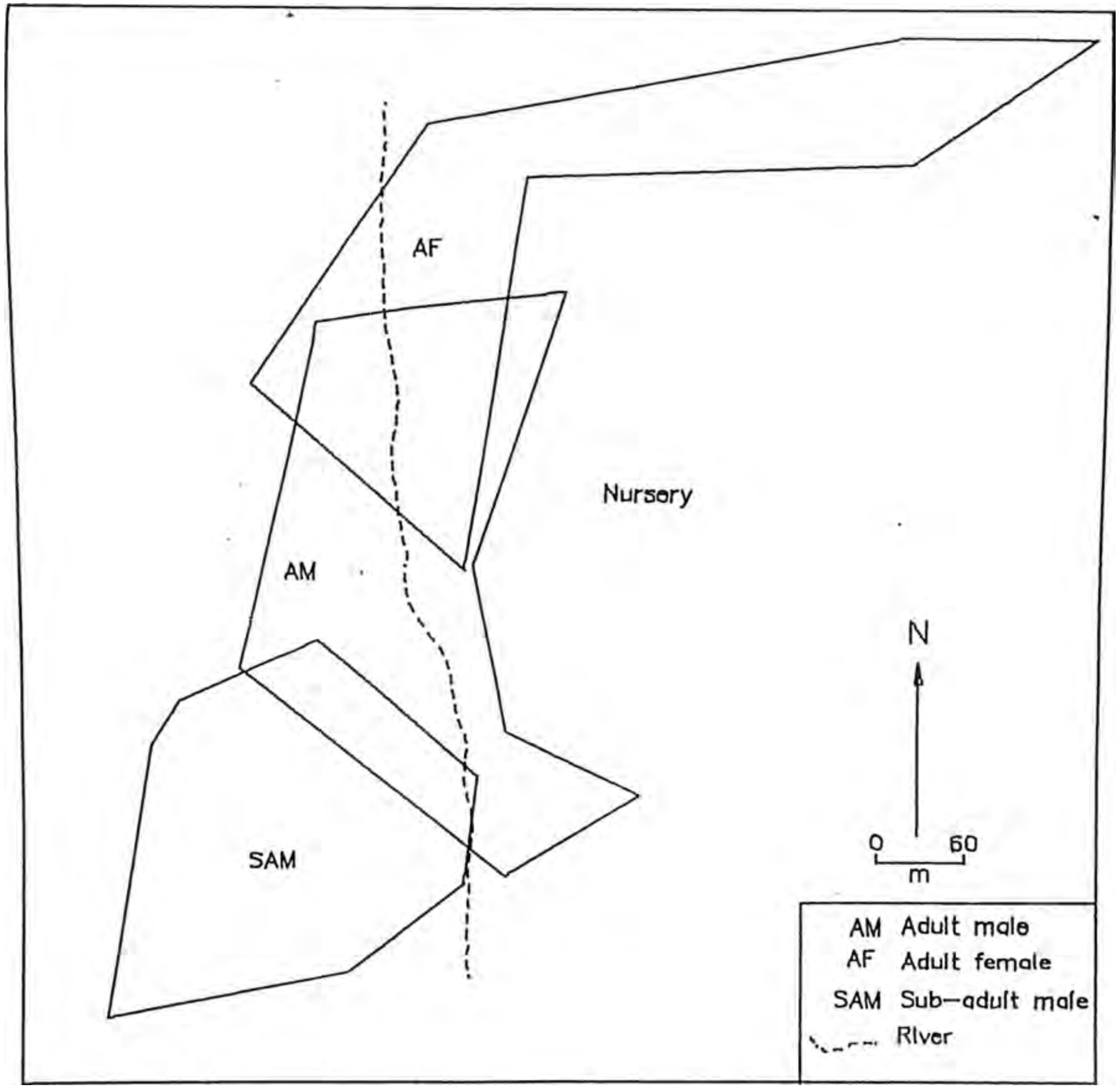


Fig. 3 Overall home areas of 3 focal individuals in Bhainsa Nala.

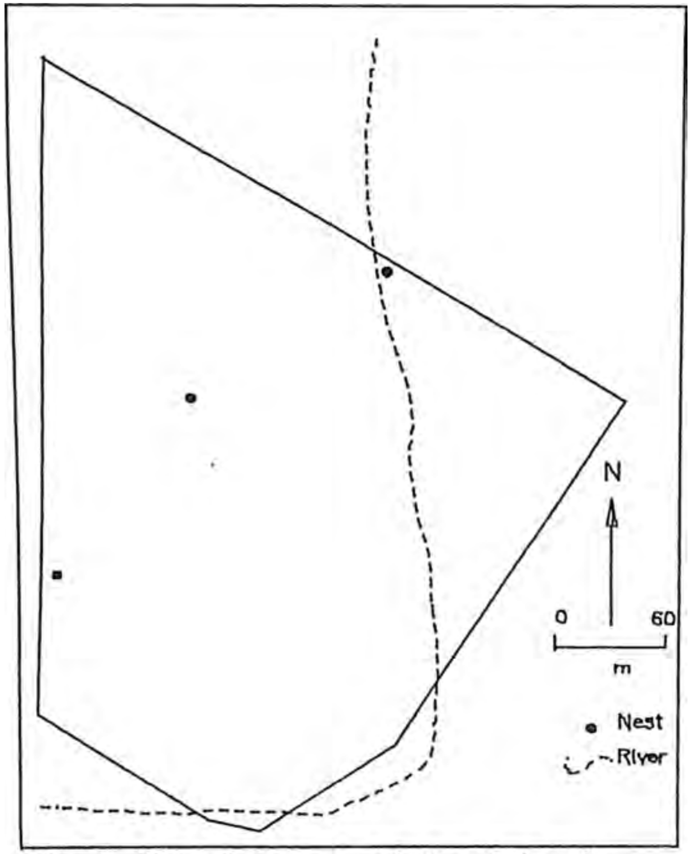


Fig. 4 Winter home area of the adult male in Churnagundi nala.

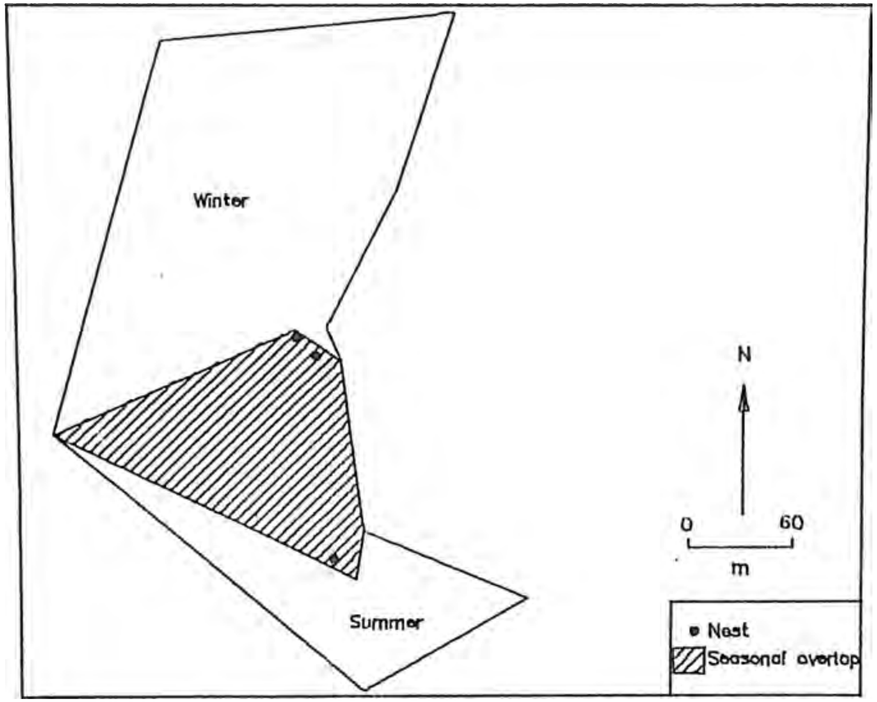


Fig. 5 Winter and summer home areas of the adult male in Bhainsà Nala

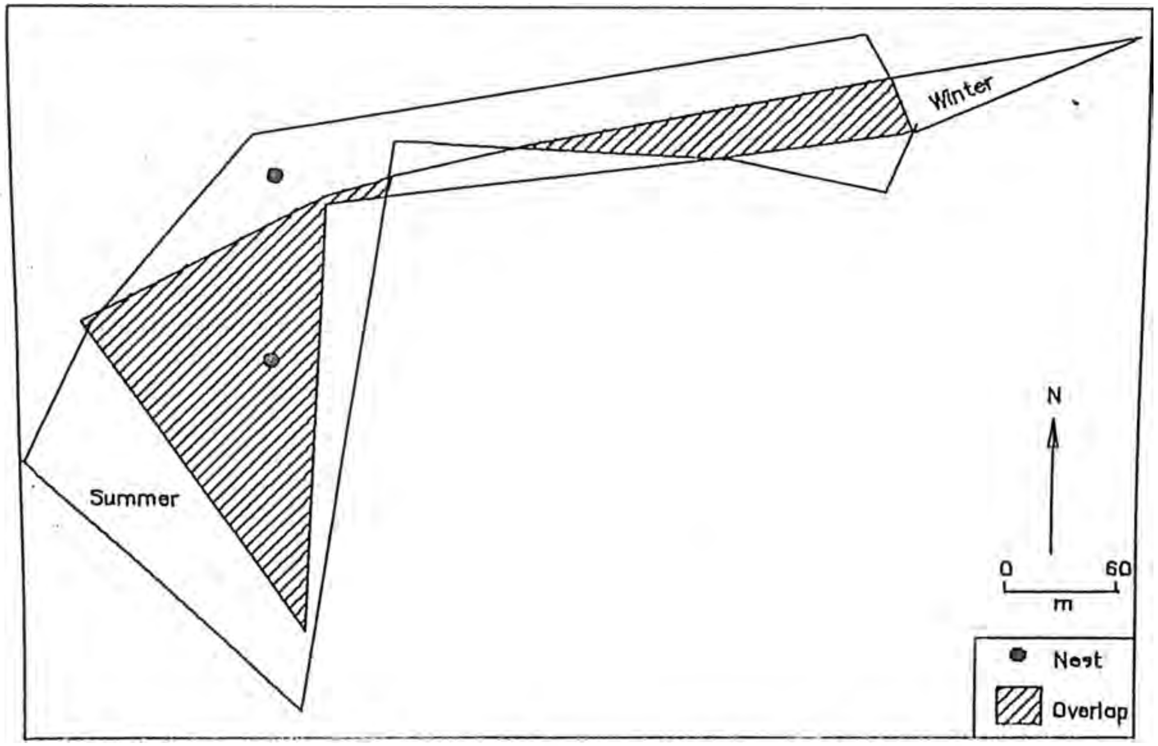


Fig. 6 Winter and summer home areas of the adult female in Bhainsa Nala

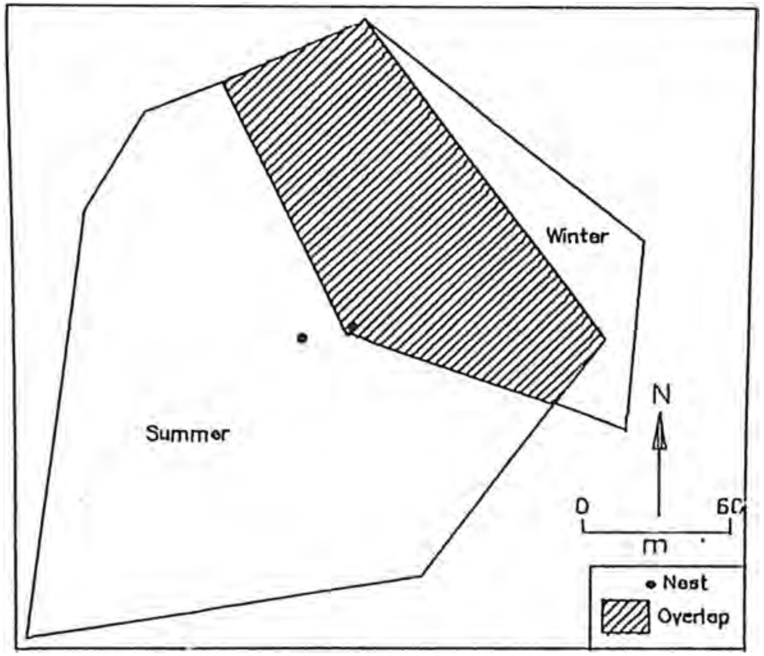
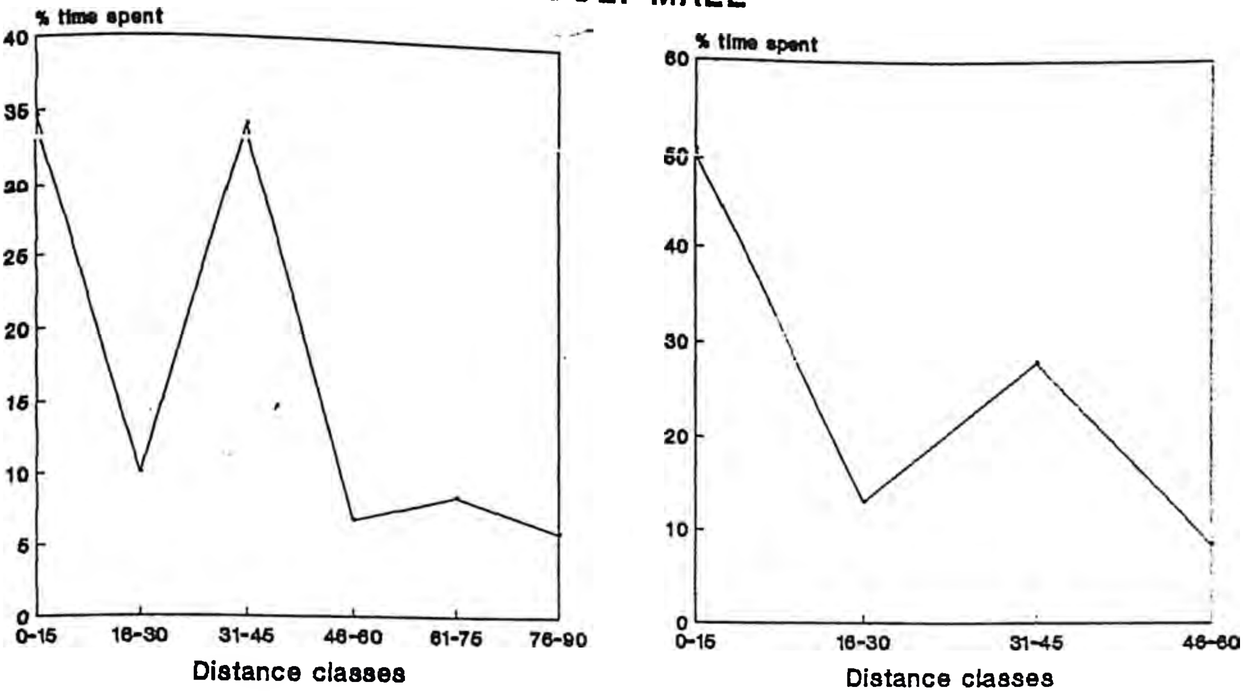


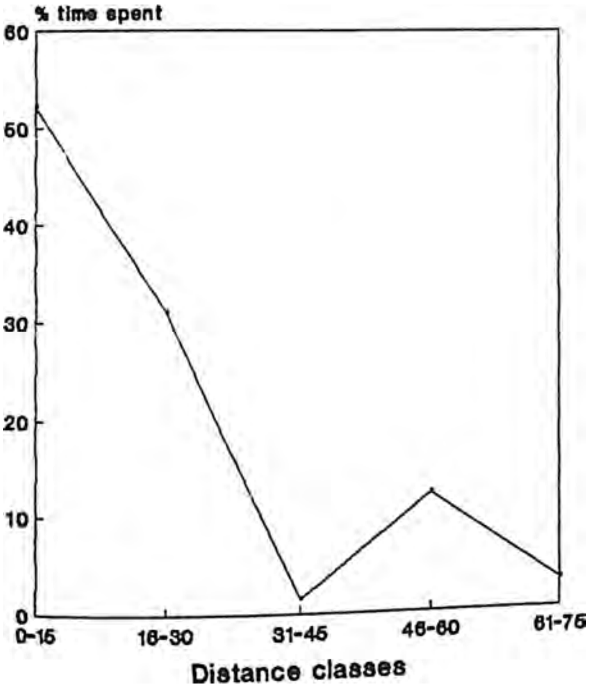
Fig. 7 Winter and summer areas of the sub—adult male in Bhainsa Nala

'FIG. 8a USE INTENSITY IN RELATION TO DISTANCE FROM DREY - ADULT MALE



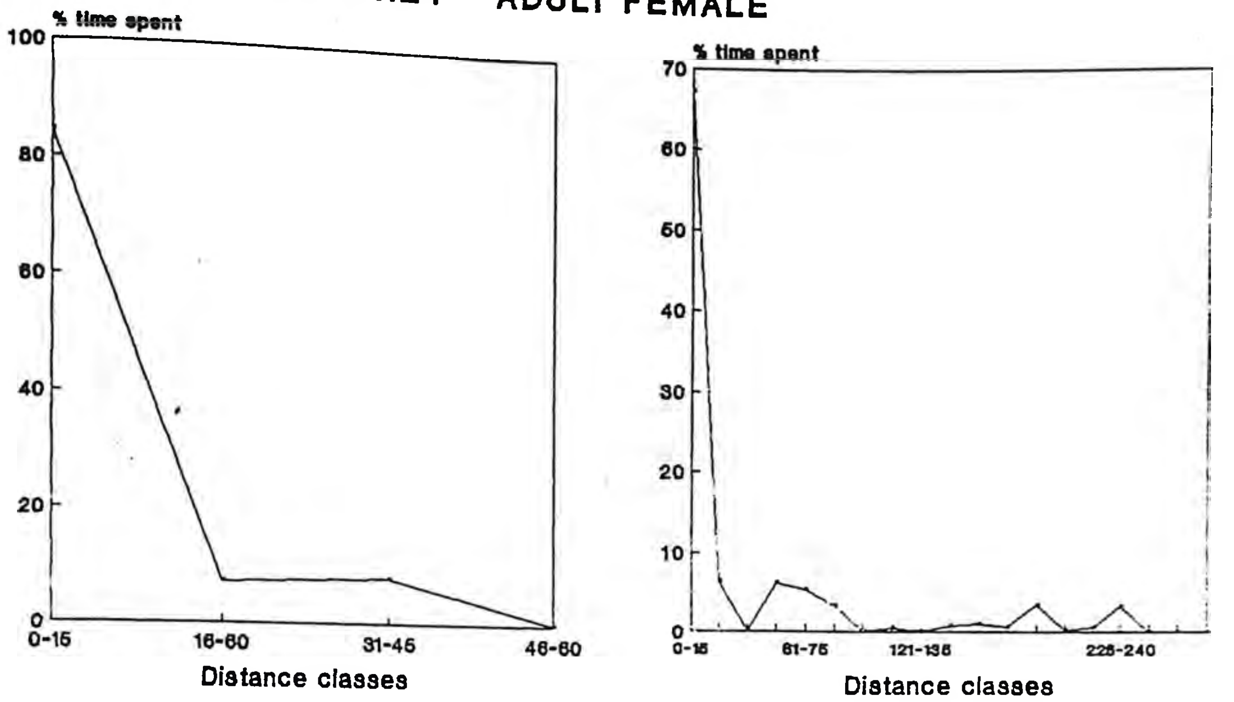
FEBRUARY

MARCH



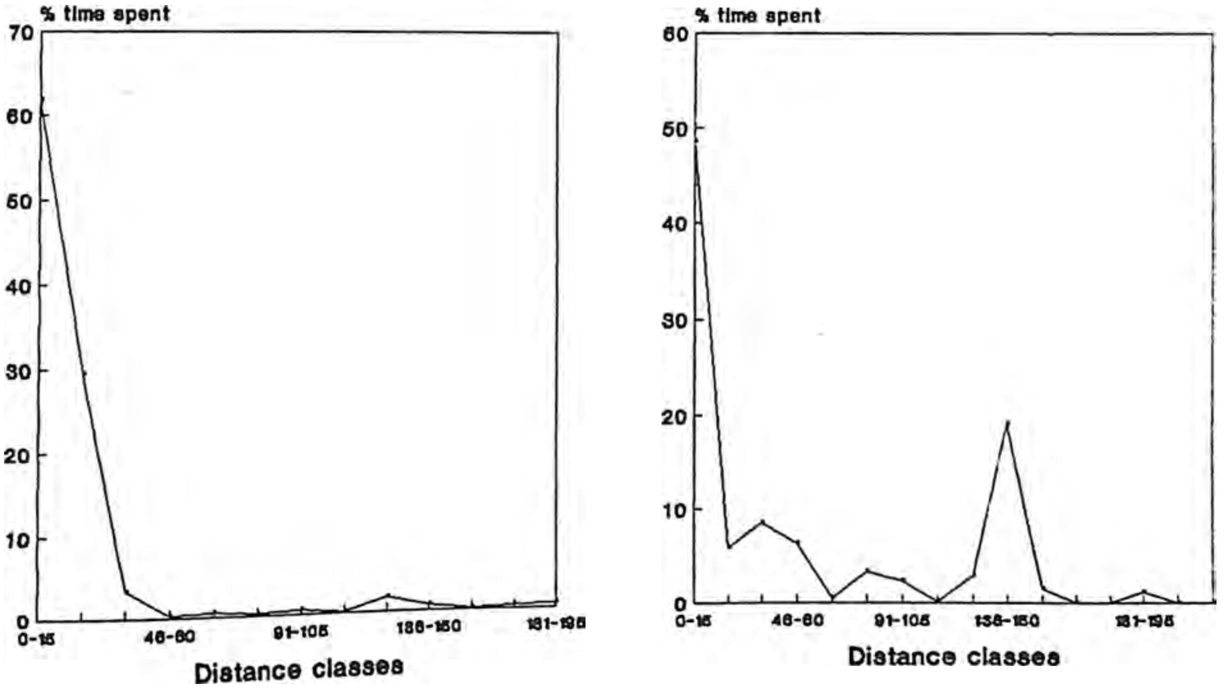
APRIL

FIG. 8b USE INTENSITY IN RELATION TO DISTANCE FROM DREY - ADULT FEMALE



DECEMBER

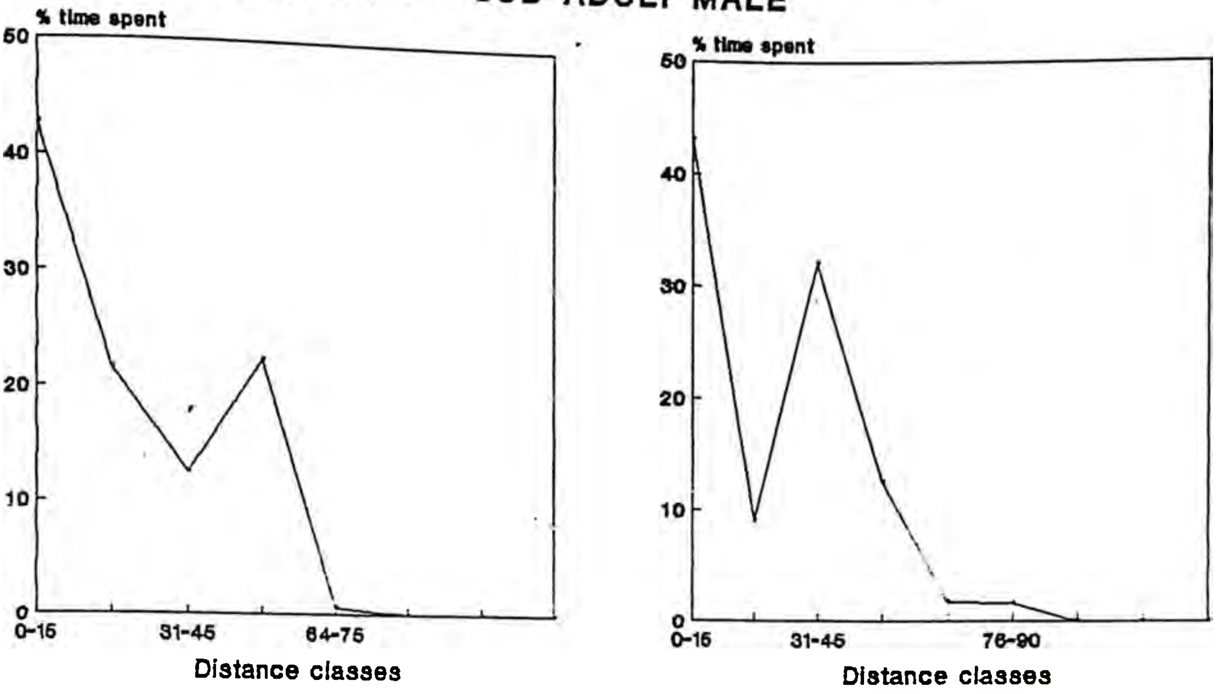
FEBRUARY



MARCH

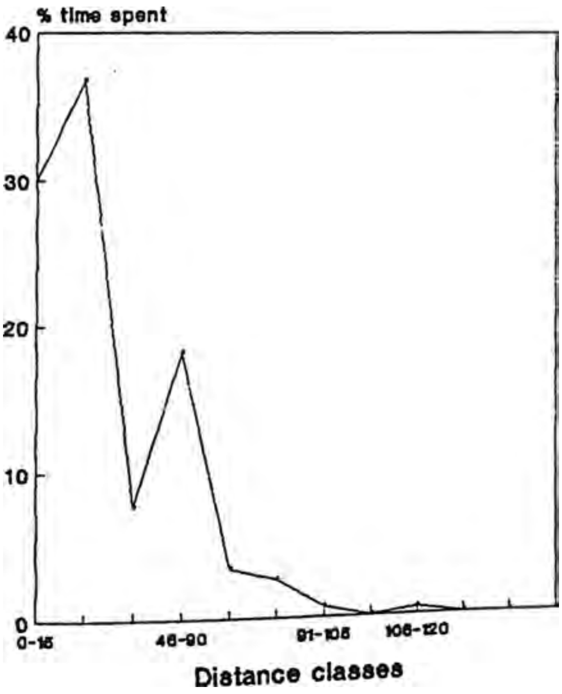
APRIL

FIG. 8c USE INTENSITY IN RELATION TO DISTANCE FROM DREY - SUB-ADULT MALE



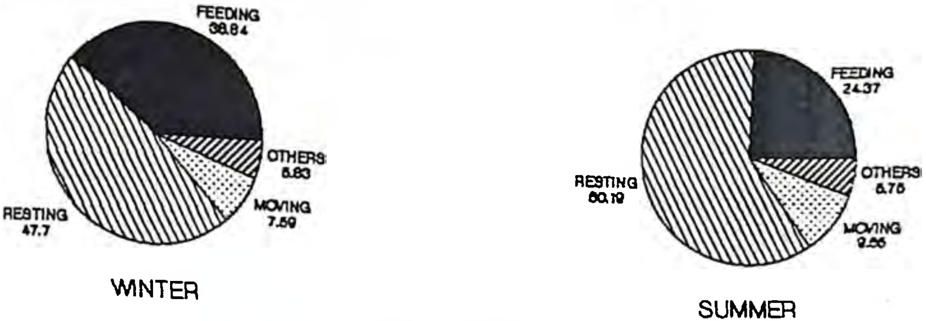
FEBRUARY

MARCH

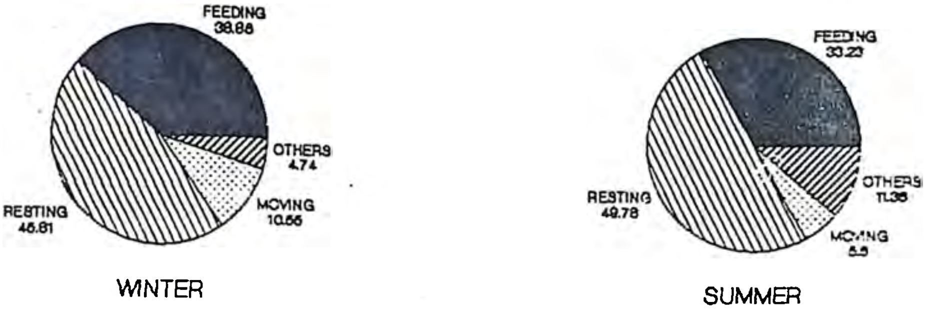


APRIL

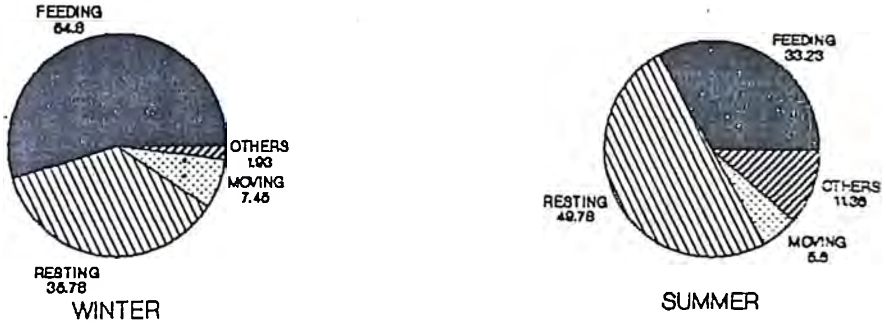
FIG. 9a ACTIVITY BUDGETS - BHAINSA NALA



ADULT FEMALE

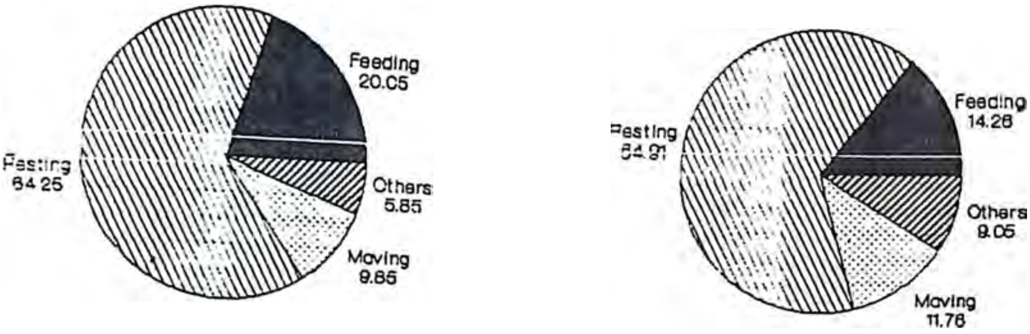


ADULT MALE



SUBADULT MALE

FIG. 9b ACTIVITY BUDGETS IN WINTER

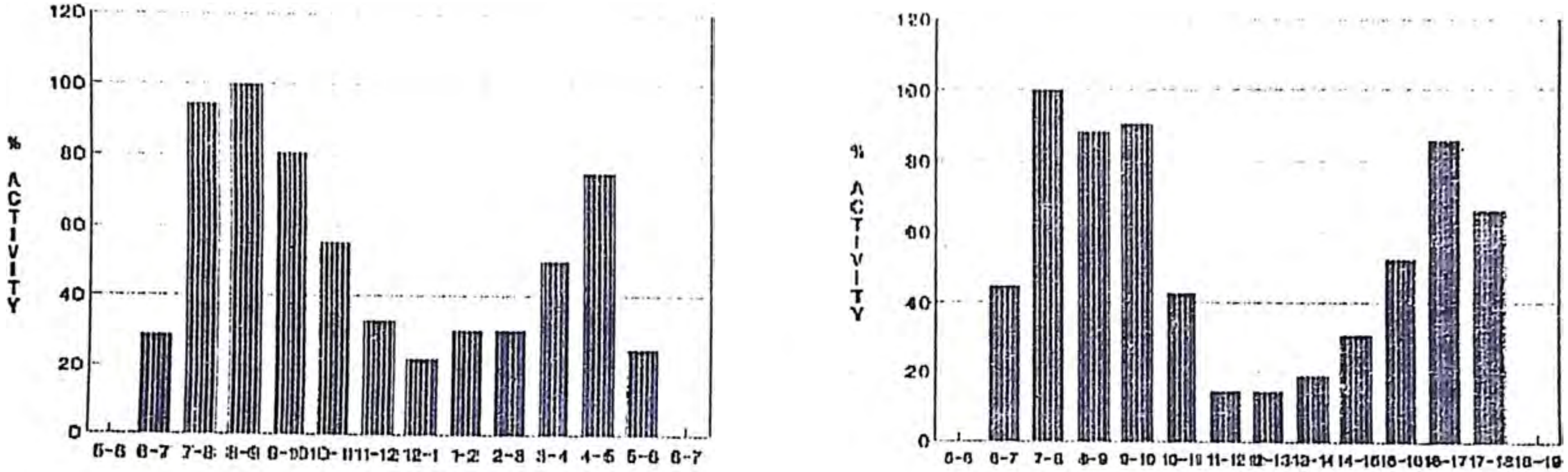


ADULT MALE

ADULT FEMALE

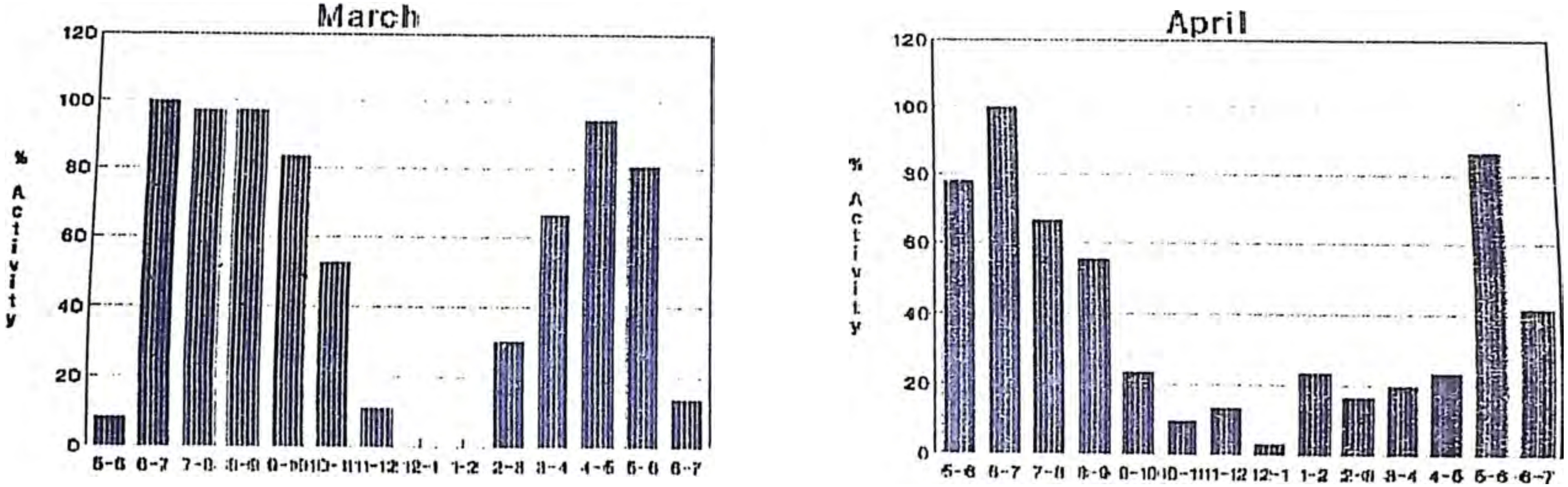
CHURNAGUNDI NALA

FIG. 10 MONTHLY TRENDS IN SQUIRREL ACTIVITY PATTERN - BHAINSA NALA



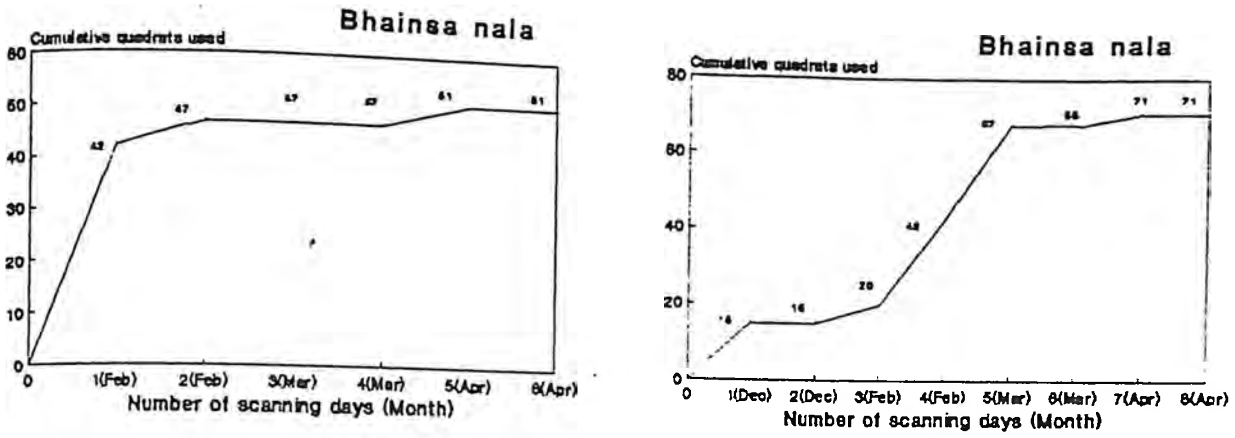
December-January

February


March

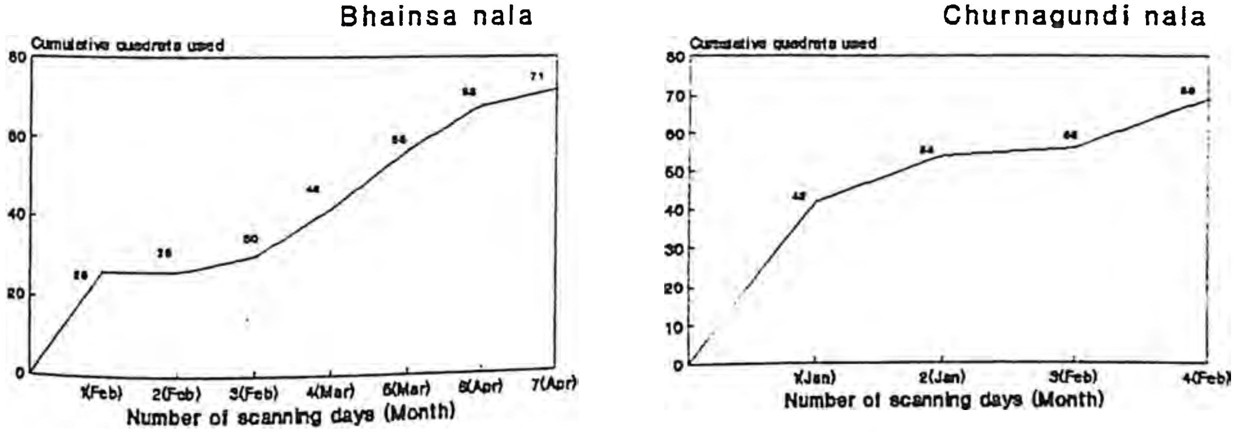
April

FIG. 11 TIME-AREA CURVES



Adult male

Adult female



Sub-adult male

Adult male

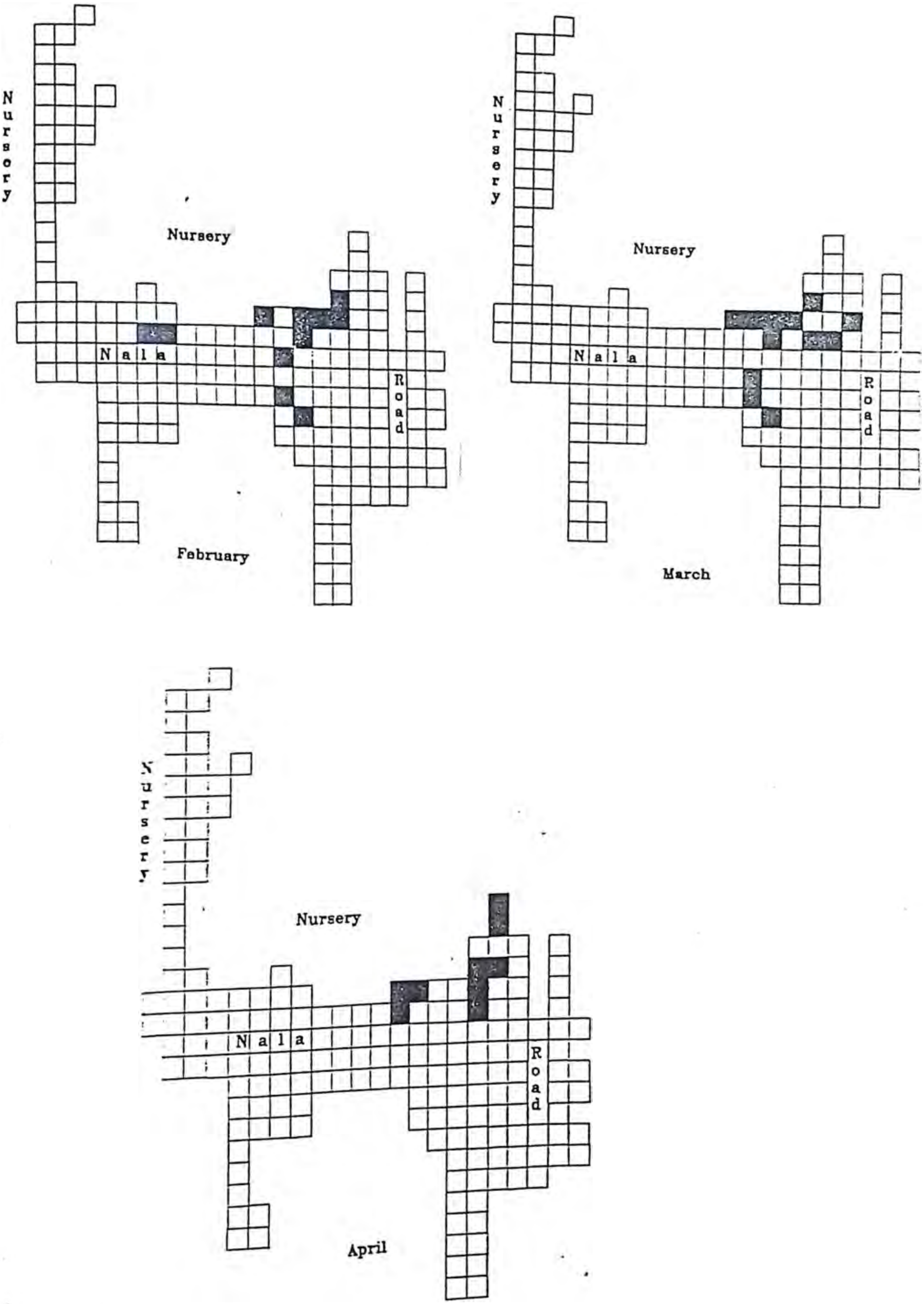
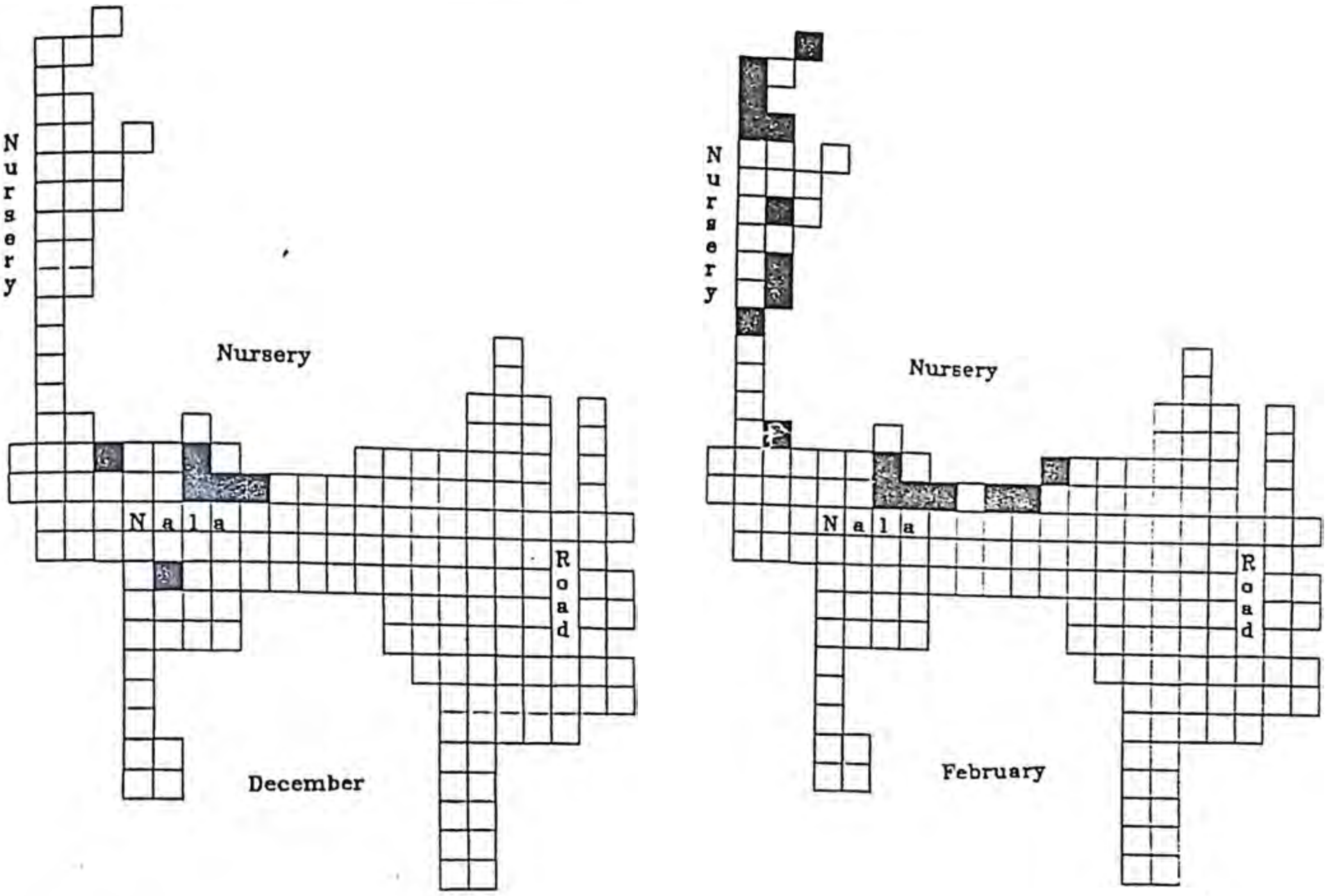


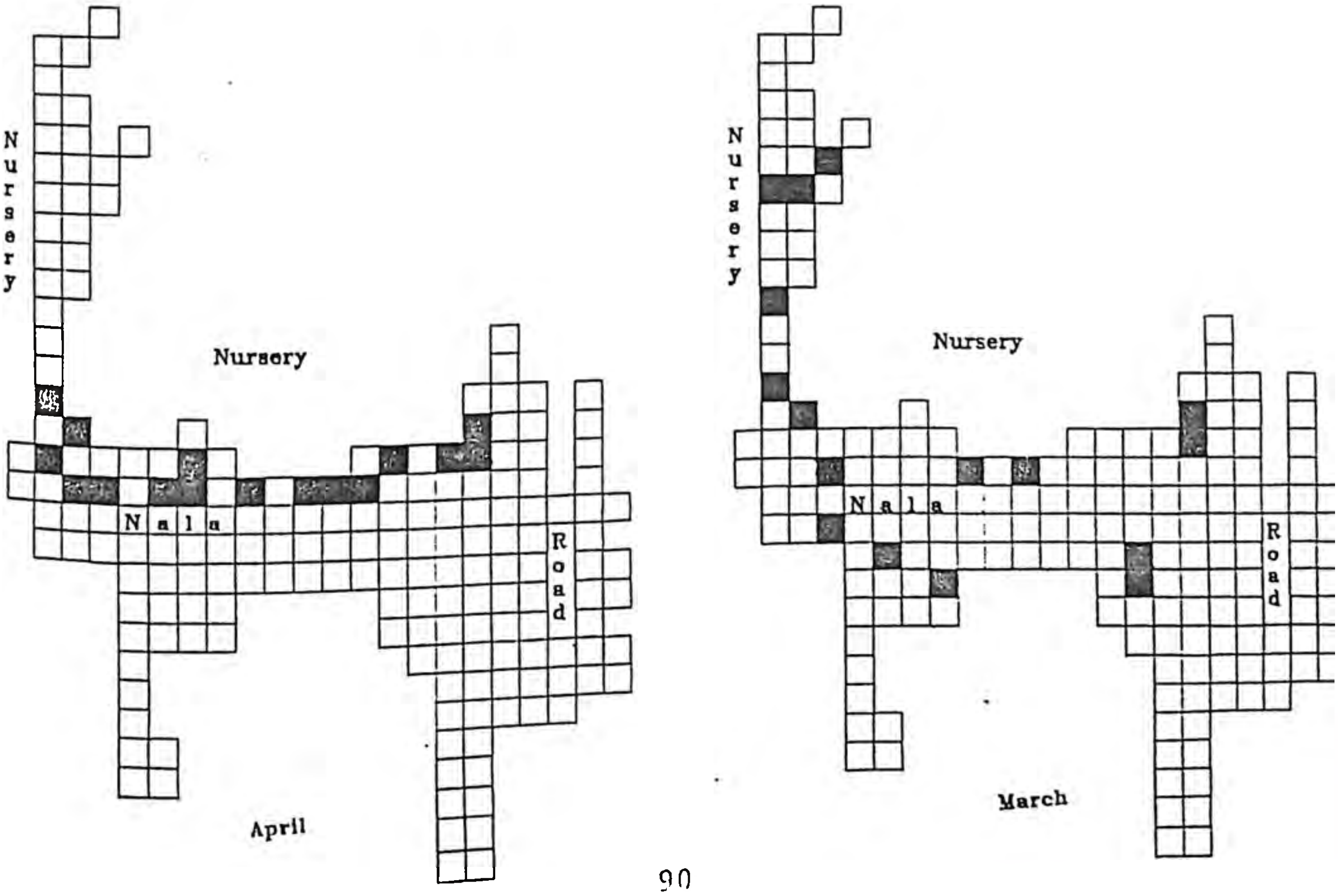
Fig. 12a Quadrats used for feeding (shaded) by the adult male in Bhainsa Nala.

Fig. 12b Quadrats used for feeding (shaded) by the adult female in Bhainsa Nala.



December

February



April

March

Fig. 12c Quadrats used for feeding (shaded) by the sub-adult male in Bhainsa Nala.

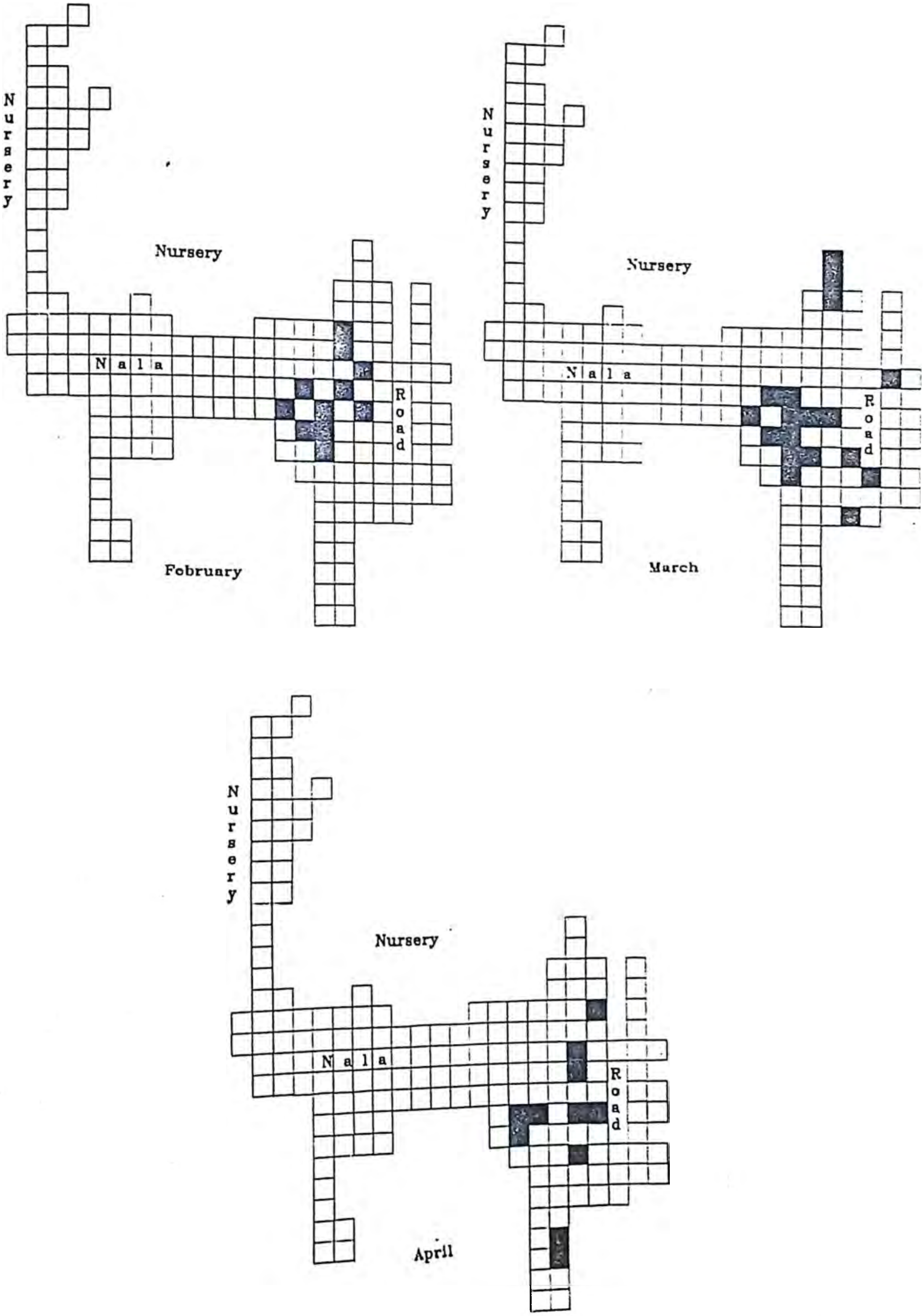


Fig. 13 A representation of the monthly use intensity patterns of the three focal squirrels in Bhainsa Nala.

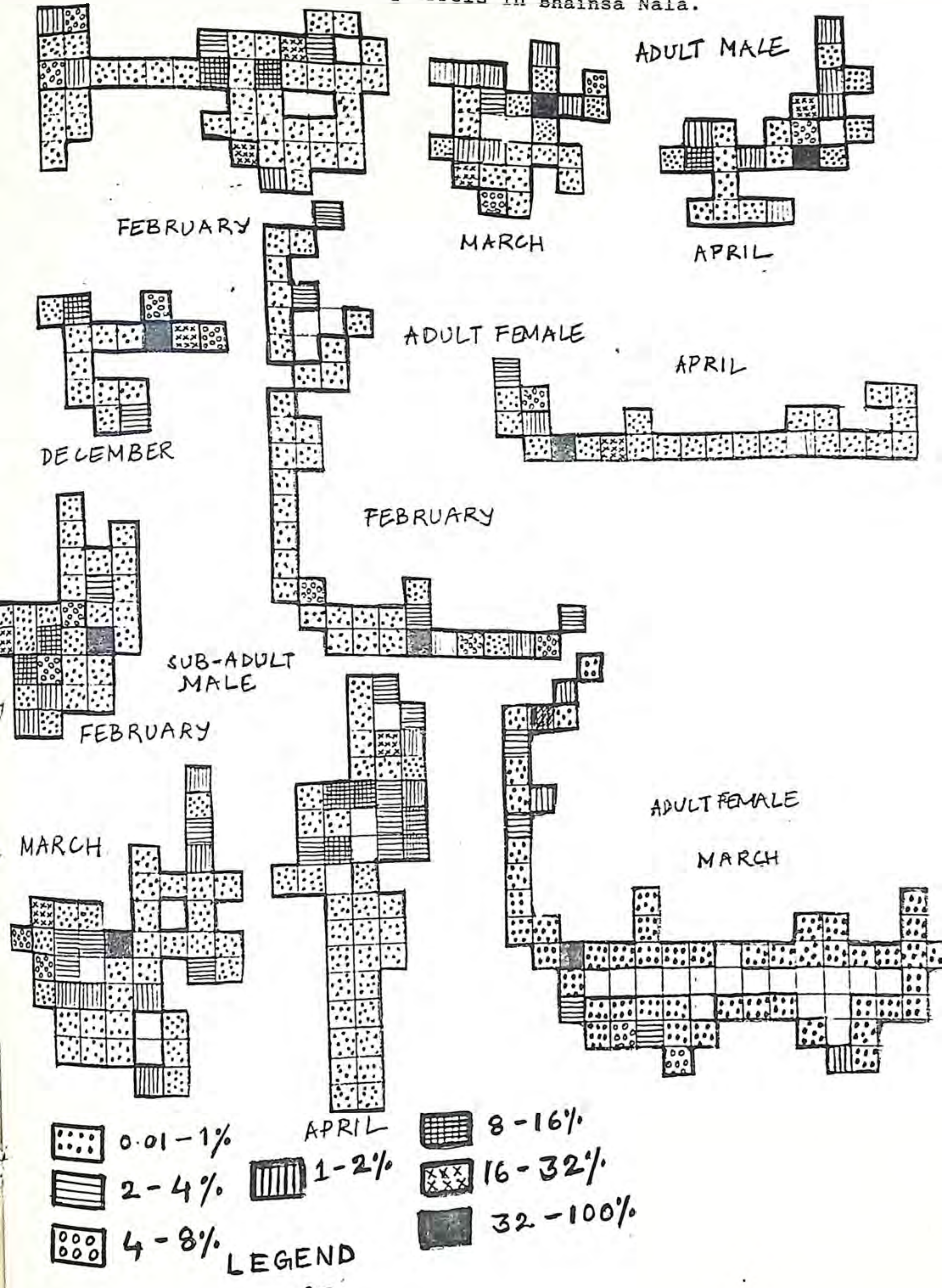


FIG. 14a LENGTH OF FRUITING PERIOD FOR FRUIT RESOURCES DURING THE STUDY PERIOD

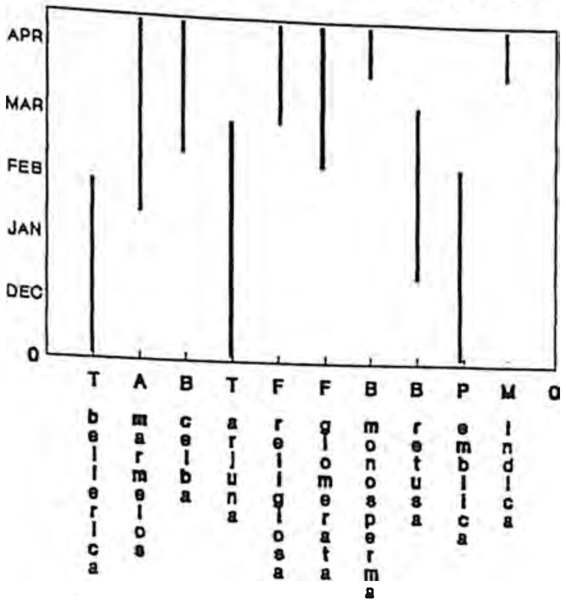
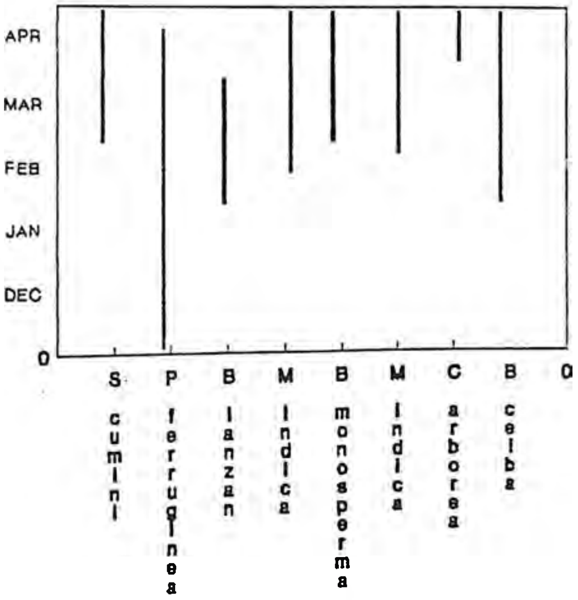


FIG. 14b LENGTH OF FLOWERING PERIOD FOR FLORAL RESOURCES DURING THE STUDY PERIOD



BHAINSA NALA

FIG. 15 Relationship between index of resource aabundance and use (% TSF) for each floral and fruit resource