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RESOURCE SELECTION AND RESOURCE PARTITIONING AMONG WILD UNGULATES IN THE TROPICAL SEMI-ARID FOREST OF RANTHAMBHORE NATIONAL PARK, RAJASTHAN

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By
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Certificate

This is to certify that *Sh. Sumanta Bagchi* of the Wildlife Institute of India, Dehradun has carried out an original research work titled **'Resource Selection and Resource Partitioning among wild ungulates in the tropical semi-arid forest of Ranthambhore National Park, Rajasthan'** in partial fulfillment of the M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot. The study was conducted under our supervision from November 2000 to June 2001. We also certify that this research work has not been submitted for the award of any other degree to any other university.

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1. Introduction

1.1. Resource Selection

Adequate quantities and quality of usable resources are a pre-requisite to sustain animal populations. Identifying the resources of key interest for particular animals has been a favourite occupation of ecologists for many decades now (Morrison *et al.*, 1998). This is important because it provides fundamental information about the survival strategies of animals and provides an insight into their decision-making processes (Rosenzweig, 1981). Differential use of shared resources is a principal factor allowing species to co-exist (Schoener, 1974).

According to 'niche' theory, species co-existing at equilibrium over shared resources; must partition the same – at least if the environment is assumed to be stable and its resources assumed to be limited (Arlettaz *et al.*, 1997). This form of differential resource use is actuated by factors like population densities, competition, natural selection, heredity and predation among others. Manly *et al.* (1993) have discussed the different theories and models ~~have been built~~ that incorporate subsets of these factors, in order to study resource selection. These have been- Foraging models (Emlen, 1966) and Habitat Selection models (Bryant, 1973). Apart from these, Habitat Suitability Indices (HSI) have been also developed to address related issues (Morrison *et al.*, 1998).

Animal populations and competition have been linked via Lotka-Volterra equations (Lawlor and Maynard Smith, 1976). Competition results when the performance of one species depletes the resources for another one. It might result in species trying to avoid each other over resource dimensions (Roughgarden, 1983). It remains difficult to measure either type in nature (Putman, 1996) without manipulative experiments (Schoener, 1983).

However, simultaneous measures of resource selection by co-existing species often reflect patterns and processes operating in animal assemblies. This approach towards studying resource-selection and resource-partitioning tries to address the Gaussian principles of competition in the framework of the Hutchinsonian niche (Hutchinson, 1957; May, 1974). Here, resources are considered niche-dimensions, upon which species either segregate or overlap (May, 1974; de Boer, 1986).

This study attempted to explore and describe the patterns of resource selection and the inter-relationships in communal niche space of four ungulate species: chital (*Axis axis*), sambar (*Cervus unicolor*), nilgai (*Boselaphus tragocamelus*) and chinkara (*Gazella benetti*) in the dry-deciduous semi-arid forests of Ranthambhore National Park, Rajasthan, India.

1.2. Review of literature

1.2.1. Habitat selection and Habitat preference

The present study is restricted to two (used and unused) out of the possible three (used, unused and available) resource-sets. In this manner, it considers 'Habitat Selection' and not 'Habitat Preference'. It is interesting to demarcate the difference between these two aspects. Habitat preference is analogous to defining an organisms 'Fundamental Niche', where it would maximize its reproductive success in the absence of competitors. Habitat selection is analogous to defining an organism's 'Realized Niche', where it actually tries to optimize its reproductive efficiency amidst several potential competitors (Armstrong and McGehee, 1976; Pianka, 1981). According to Johnson (1980), 'selection' is the process in which an animal chooses a resource; and 'preference' is the likelihood that a resource will be selected if offered on an equal basis with others. Thus habitat selection can be looked at as a combination of learned as well as instinctive responses to certain environmental cues (Rosenzweig, 1981).

1.2.2. Design of Resource selection studies

Given the decision to study resource selection in a particular animal assembly, the subsequent step is to determine the scale of selection to focus on (Johnson, 1980). Resource selection occurs in a hierarchical fashion- from the geographic range of a species to individual home ranges, to general habitat features within the home range, to specific features within the general habitat features (Johnson, 1980). Some study designs address multiple scales at the same time (Hall and Mannan, 1999). The present study accosts two levels of selection, namely, general features in the habitat and specific features within the same. Manly *et al.* (1993) have considered the design of such studies in the following manner:

a) Sampling Protocol:

Resource selection can be detected and measured by comparing any of the three possible sets, *viz.* 'used', 'unused' and 'available', of resource units. Based on this three sampling protocols have been identified -

- Protocol A, where random samples of available units are measured, along with a random sample of used units.
- Protocol B, where available units are randomly sampled along with a random sample of unused units.

- Protocol C, where used units and unused units are sampled independent of each other.

b) Design:

- Design I, that operates at the population level and individual animals are not identified. Lagory *et al.* (1985) used this design to study the white-tailed deer (*Odocoileus virginianus*) in North America.
- Design II, where uses of resources are measured based on individually identified animals, but availability is measured at the population level. The elk (*Cervus elaphus*) was studied in North America by McCorquodale *et al.* (1986) using this design.
- Design III where identified animals are used to measure at least two out of the three units: used, unused and available units. Rolley and Warde (1985) studied bobcats (*Felis rufus*) in North America using this design.

Each of these sampling protocols (A, B, C) can be implemented with any of the above three designs (I, II, III) to carry out a study. For the present study, data collection was done on the basis of Design I + Protocol C, as will be discussed subsequently. In this effect, animal populations were looked at for usage and non-usage of resources at a scale that has been already been mentioned. So to summarize the design of the present study:

Sampling: used and unused units
Design: type I, population level
Scale: i) general features in the habitat and
ii) special features in the habitat

1.2.3. Resource partitioning in animal communities

As mentioned earlier, partitioning of resources is one way in which similar species can co-exist (Schoener, 1974). It is postulated that in most animal communities, resources are first partitioned in terms of habitat and then by food. Temporal partitioning comes third (Schoener, 1974; Toft, 1985). Another aspect of resource partitioning is that species tend to overlap with each other in complementary resource dimensions. For example, if two species are overlapping on an important resource X, they show separation on another critical resource Y, thus enabling both to co-exist (Dunbar, 1978; Green, 1987). Such patterns can be investigated by simultaneous measurements of resource selection by co-existing species.

1.2.4. Ungulate- Habitat relationships

Most emphasis on studying ungulate-habitat interactions have been given to the animals of the African Savannah (e.g. Ferrar and Walker, 1974; Hirst, 1975; Dunbar, 1978; Jarman and Sinclair, 1979; Ben-Shahar and Skinner, 1988); in the North American continent (e.g. Mackie, 1970; Irwin *et al.*, 1983; Edge *et al.*, 1987; Jenkins and Wright, 1988) and also in Europe (e.g. Schwartz and Ellis, 1981; Putman, 1986; Pratt *et al.*, 1986; Gordon and Illius, 1989). In comparison, the examples from the Indian-subcontinent are much fewer. These studies can be looked at in the context of separate geographic zones, *viz.* the Himalayan ungulate assemblages, the ungulates of western and peninsular India and the species residing in the arid zone.

- **Himalayan region**

Green (1987) looked at the ecological separation of four sympatric ungulates- musk deer (*Moschus chrysogaster*), goral (*Nemorhaedus goral*), serow (*Capricornis sumatraensis*) and sambar in Kedarnath Wildlife Sanctuary, Uttar Pradesh (now Uttaranchal). Results suggested that resource partitioning was achieved between any species-pair by restricting overlap to any one of the two dimensions, *viz.* habitat and food. There was an inverse relation between overlap in habitat use and overlap in diet, which enabled them to coexist.

Sathyakumar (1994) looked at relationships between musk deer, Himalayan tahr (*Hemitragus jemlahicus*), serow, sambar and barking deer (*Muntiacus muntjak*) in the same study area as Green (1987). Results suggested that ecological separation between the five species was achieved by differential use of altitude, which was in agreement with the findings of Green (1987).

Bhatnagar (1997) studied relationships between domestic livestock and ibex (*Capra ibex*) in the Trans-Himalayan region. Ecological separation was achieved largely by differential use of altitude during summer and winter. However, they overlapped in habitat use during spring and autumn. But ibex preferred areas closer to escape terrain and used steeper slopes than livestock.

- **The Western and Peninsular regions**

Martin (1982) investigated interspecific relations between barasingha (*Cervus duvauceli branderi*) and chital in Kanha National Park, Madhya Pradesh. He found no evidence for niche separation or feeding succession between the two species and suggested competitive exploitation of the key food species (*viz. Bothriochloa odorartum.*

Saccharum spontaneum and *Themeda triandra*) between chital and barasingha. Chital being more generalist utilized other habitats as well as alternate food species with higher efficiency than barasingha.

Khan (1996) studied habitat relationships of chital, sambar and nilgai in Gir Lion Sanctuary and National Park, Gujarat. Results showed that the three ungulates preferred certain vegetation types over others and were spatially segregated. Their overall distribution pattern ensured that high density of one species does not coincide with that of another.

Mathur (1991) studied three sympatric ungulates- chital, sambar and nilgai, in three different areas, Sariska National Park, Rajasthan; Tadoba National Park, Maharashtra and Kanha National Park, Madhya Pradesh. Mechanism allowing coexistence was discussed in terms of habitat selection. Resources were partitioned mainly by use of different habitats. Sambar used forest-woodland habitat and well-wooded moderately steep slopes close to perennial water. Nilgai used flat open areas with low canopy cover and high shrub cover. Chital used the woodland-grassland 'edge' habitat having moderate canopy cover and high grass cover.

Sankar (1994) studied three sympatric ungulates *viz.* chital, sambar and nilgai along with domestic livestock, in Sariska Tiger Reserve, Rajasthan. He found that all the three species had moderate to high population densities in the study area, but the usage of different vegetation types was not uniform and they preferred some vegetation types over others. The wild ungulates avoided areas that were used by livestock. Eroded areas were avoided by nilgai and chital while sambar and chital avoided lopped areas. Chital preferentially used *Zizyphus* woodland and *Butea*-mixed forest. Sambar preferred

Zizyphus woodland and *Boswelia-Anogeissus* forest. Nilgai used *Zizyphus* woodland and degraded areas more than others.

Haque (1990) studied chital, sambar, nilgai and blackbuck (*Antilope cervicapra*) alongside feral cattle in Keoladeo-Ghana National Park, Rajasthan. During the pinch period of summer, the species were seen to be most separable in habitat use. Overall, sambar was using a distinct guild in all seasons, utilizing a considerable amount of browse. The other species showed some overlap in habitat use in all seasons.

- **The Desert zone:**

Goyal *et al.* (1986) studied food preferences and habitat use of chinkara and blackbuck near Jodhpur, Rajasthan. They found, chinkara preferring *Crotolaria-Tephrosia-Zizyphus* dominated regions and blackbuck opting for *Tephrosia-Prosopis* type of vegetation, leading to spatial separation. Chinkara and blackbuck differed considerably in diet as well. Chinkara, was predominantly seen to be a browser and concentrate feeder, utilizing protein-rich pods in considerable amounts. Blackbuck on the other hand was found to be predominantly a grazer and roughage feeder.

Kunhunu (1989) studied dietary relationships between chinkara, blackbuck and nilgai along with domestic livestock in Jodhpur, Rajasthan. He found evidence of food resource partitioning between the above species, which was achieved by diet selection processes.

- **Recent trends in Ungulate-Habitat studies in India**

The majority of the studies dealing in animal-habitat interactions in India have been in univariate framework. These studies have contributed significantly to the body of knowledge over understanding the patterns of resource selection. But as common to all univariate approaches, they have overlooked the effect of interaction among habitat features. Madhusudan and Johnsingh (1998) have elaborated these aspects while demonstrating the use of ordination techniques for describing Nilgiri tahr (*Hemitragus hylocrius*) habitat utilization. Sharma and Johnsingh (1996) also used ordination techniques to describe habitat relationships of chital, sambar and nilgai in Gir Lion Sanctuary. Similarly, Mathai (1999) investigated effect of human disturbance on habitat use by ungulates in Panna Tiger Reserve by ordination methods.

This study takes into account inter-relationships and relies on multivariate analytical techniques to describe patterns.

2. Objectives

The purpose of the study was to find answers to the following questions:

i) What are the patterns in habitat selection in the study species?

ii) What factors influence habitat selection and usage by these species?

iii) What is the extent of ecological separation among the four species of ungulates?

iv) Are there any relationships between resource selection patterns and abundance of the species?

In this effect, the following objectives had been set:

1. to estimate the densities of the four species in the study area and determine their relative abundance,
2. to identify different habitat types within the study area based on vegetation and terrain features,
3. to find out if there are differences in the relative usage of various habitat types by the four ungulate species, i.e. macro-level resource selection,
4. to find out finer level of habitat selection in terms of use of specific resources, and importance of individual factors in habitat selection, i.e. micro-level resource selection.
5. to assess the extent of overlap and/or isolation in the resource use patterns; in order to understand the means and modes of resource partitioning,
6. to identify seasonal trends. (if any), in patterns of resource use and overlap and
7. to explore the possible relationships between niche patterns and species abundance.

3. Study Area

3.1. General

The present study was carried out between November 2000 and April 2001, at Ranthambore National Park; located between 25^0 54′ N – 26^0 12′ N latitude and 76^0 22′ E – 76^0 39′ E longitude; in Sawai Madhopur district of Rajasthan (Fig. 1). In 1973, Ranthambore was declared as one of the first nine Tiger Reserves under 'Project Tiger'. The National Park was notified in 1980 and covered 392 sq. km. of area. Today, Ranthambore Tiger Reserve is spread over 1334 sq. km. of which 274 sq. km. of area is given the management status of the 'core area'. Geologically, Ranthambhore shows elements of the Aravali and the Vindhya hill ranges.

3.2. Vegetation

The vegetation of Ranthambore is a typical representative of dry-deciduous *Anogeissus pendula* forest. Champion and Seth (1968), considered the vegetation of Ranthambore as being comprised of: i) *Tropical Dry Deciduous Forest* and ii) *Tropical Thorn Forest.* Apart from *Anogeissus*, the other species commonly found are *Sterculia urens*, *Boswellia serrata*, *Acacia leucophloea*, *Cassia fistula*, *Butea monosperma*, *Diospyros melanoxylon*, *Cordia myxa*, *Mitragyna parviflora* and *Syzigium cumini.* The slopes of the Aravali show consolidated rocks and are often seen to be under thick *Anogeissus* cover. On the other hand, the Vindhya slopes show flaking stones and support much less tree cover. Frequently, these slopes are seen to, be supporting grassy-savanna type of vegetation. Sites from where villages have been relocated in the past, have gone through vegetation successional stages and are today seen to exhibit *Acacia*-mixed woodland serai stages.

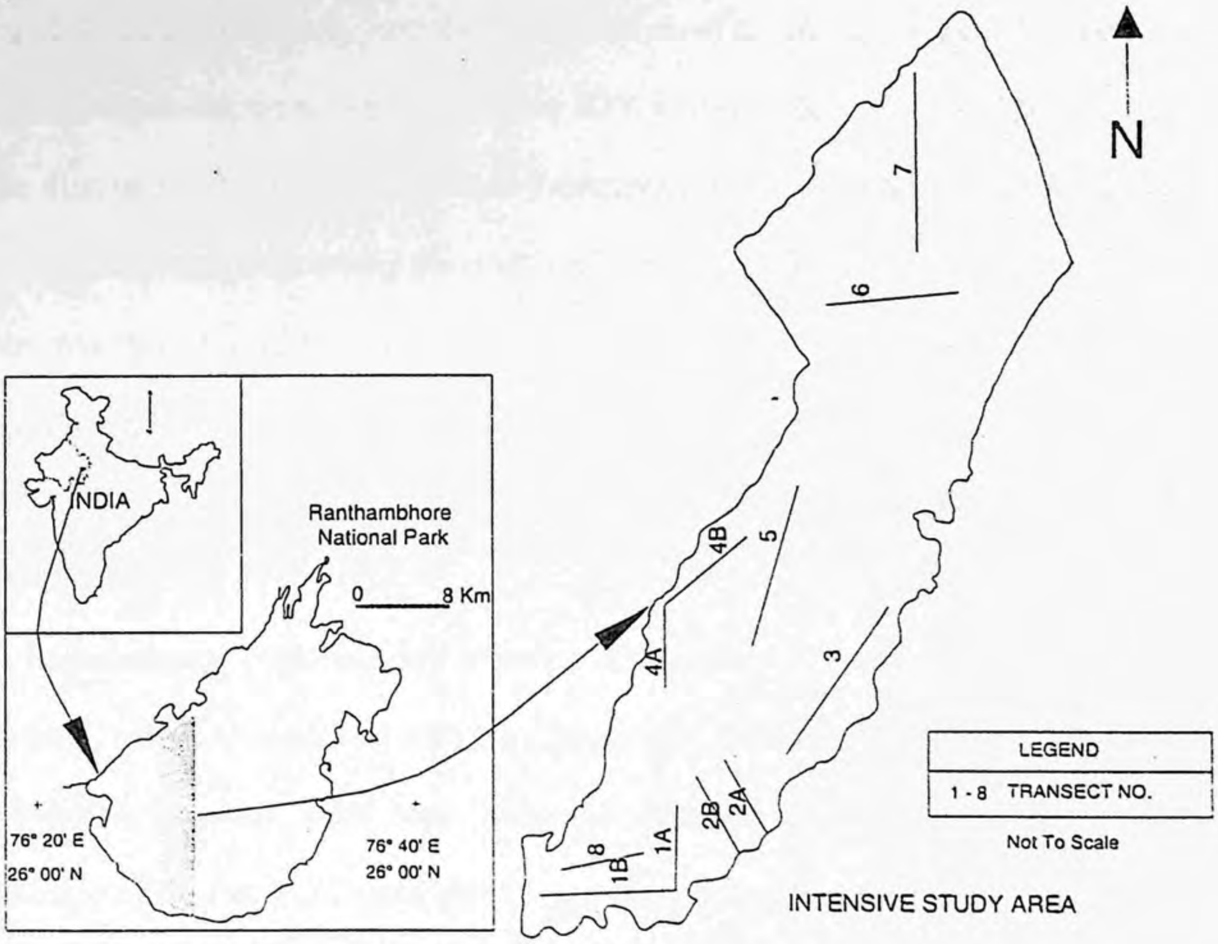

Figure 1. Map showing study area (Ranthambhore National Park) and Line transects in the Intensive Study Area.

3.3. Climate

Ranthambore is characterized by subtropical dry climate with four distinct seasons. March to June is summer, followed by monsoon in July-August, a short post-monsoon during September-October and winter from November to February. The average annual rainfall is about 800 mm, most of which is received during July-September. The present study was conducted between November 2000 to April 2001, wherein two seasons could be distinguished: Winter (November-February) and early Summer (March-April). The minimum temperature during the study period was experienced during January (3^0C) and the maximum during April (46^0C). Frost was observed regularly in winter, but only in the vicinity of the lakes and water holes. During the study period, the region received 24 mm. of rainfall, mostly during late-afternoon dust storms in April. (Source: local newspapers).

3.4. Fauna

Ranthambhore National Park supports five species of wild ungulates, *viz.* chital, sambar, nilgai, chinkara and wild pig (*Sus scrofa).* Other mammals like common langur (*Presbytis entellus*), sloth bear (*Melursus ursinus*), ratel (*Mellivora capensis*), and porcupine (*Hystrix indica*) and hare (*Lepus nigricollis ruficaudatus*) are also found. The large predators are tiger (*Panthera tigris*) and leopard (*Panthera pardus*), apart from which, striped hyaena (*Hyaena hyaena*), jungle cat (*Felis chaus*), caracal (*Felis caracal*), common palm civet (*Paradoxurus hermaphroditus*), ruddy mongoose (*Herpestes smithii*) are also found. Wild dogs (*Cuon alpinus*) are occasionally encountered. There are some recent reports of the presence of wolf (*Canis lupus*) in the park. The present study focussed on four ungulates, *viz.* chital, sambar, nilgai and chinkara, which are known to occur in moderate to high densities in the park (Kumar, 2000).

3.5. Intensive study area

An 'Intensive study area' (ISA) was selected in Madhopur Range, stretching from *Rajbagh* in the north to *Bodal* village in the south (Fig. 2). This covered approximately 34-sq. km. of area encompassing all major terrain and vegetation features found in the park. Human activity in the ISA was in the form of regulated tourism, restricted pilgrimage by local people and illegal livestock grazing in the southern portions. Villagers sometimes brought cattle, buffaloes, goats and camels for grazing inside the park boundaries. There were two villages close to the ISA, *Mordungri* and *Bodal*, both located near the southern boundary. The ISA was made up of eleven sites. These sites were recognized on the basis of their local names and were considered to be the sampling units for the purpose of the present study. Two of the major water sources in the park, in form of perennial lakes (*Rajbagh* and *Padam talav*), fell inside the ISA. Apart from these, there were several other natural and artificial waterholes located inside the ISA.

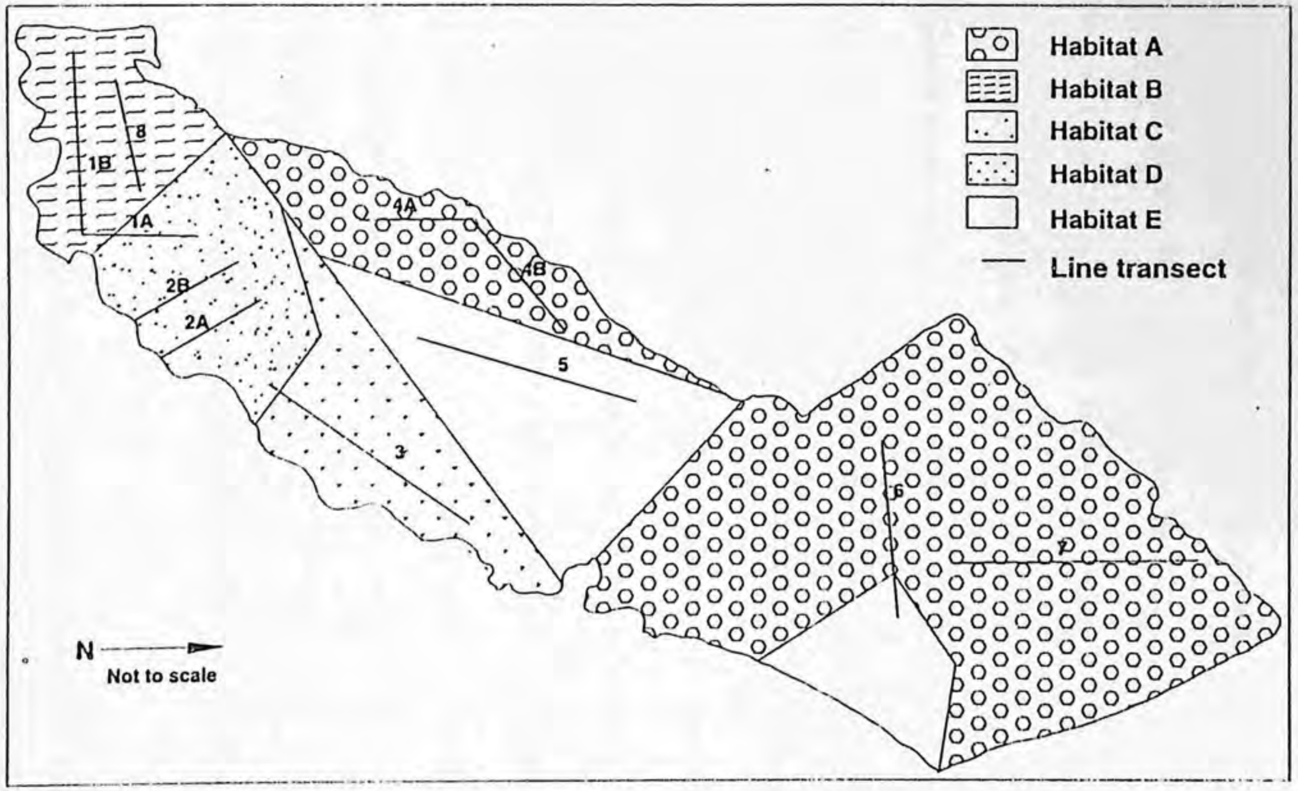

Figure 2: Various Habitat types (A to E), along with Line transects (1 to 8) in the Intensive Study Area in Ranthambhore National Park.

Description of Habitat types
Type A: = *Anogeissus* forest with *Grewia*
Type B: = *Anogeissus-Diospyros* forest with little shrub layer
Type C: = *Anogeissus* forest with *Capparis-Dichrostachys* scrub
Type D: = *Acacia-Zizyphus-Anogeissus-Butea* woodland
Type E: = Grassy slopes and plateaus

4. Methods.

4.1. Data collection

4.1.1. Animal distribution and abundance

4.1.1.1. Direct evidences

Eight line transects were cut and marked, with length varying from 1.5 to 2.8 km. in different parts of the study area, covering all vegetation types and terrain features. The total length of the line transects were 19.5 km. Each line transect was walked seven times in each season during winter and summer. In this manner, each season had 136.5 km. of walk and in the entire study period there were 273 km. of walk. Transects were walked by two observers, myself and one field assistant. Walks were carried out at a steady pace of 1.5 to 2 km. per hour; depending on terrain. In this manner, no walk took more than two hours to be completed. Walks were carried out during morning (four times in a season) and evening (three times in a season); periods during which animals were most active. In winters, walks were started 1.5 to 2 hours after sunrise and 2 to 2.5 hours before sunset. In summers, walks were started 0.5 to 1.0 hours after sunrise and 1.5 to 2.0 hours before sunset. The reason behind these adjustments being the prevalent weather conditions that influence animal activity patterns (Chakrabarty, 1991).

During transect walks, on every animal sighting, the following aspects were noted down-

i) Species and group size: a single animal, or one or more animals of the same species, observed within 30 m. of each other were considered as a group.

ii) Position: observations of animal clusters were noted for whichever segment (200 m. segment) of a transect they were sighted.

iii) Sighting angle: using a hand-held compass (Suunto *KB 20*), the bearing of the animal cluster was taken. This was done by using the approximate centre of the group as the point of reference for observation.

iv) Sighting distance: using a laser range finder (Bushnell *Yardage Pro* 400), the distance to the centre of group was measured from the point of observation. On some occasions, due to unavoidable reasons, measurements were taken of any recognizable object closest to the animals.

4.1.1.2. Indirect evidences

Along the line transects, at every 200 m. interval, a 10 m. radius circular plot was laid for determining rate of pellet deposition by the study animals. In addition to the four study species, the presence or absence of dung or pellets of domestic livestock was also recorded. All dung/pellets were cleared from a plot at the beginning of the study and left for further deposition to occur. A cluster of more than 10 pellets of a particular species was considered a pellet-group and indicated a single instance of habitat use (Rogers *et al.*, 1958; Neff, 1968). Identification of species from pellets was done instantly by observing shape and size characteristics (**Appendix I**). Dung/pellet deposition was counted during mid-winter, end of winter and lastly at the end of the study period. Due to logistic constraints, all plots could not be given equal number of days for deposition. For winter, plots were given 85 to 95 days for deposition and in summer they were given 50 to 55 days. Thereafter all counts were standardized for a period of 100 days before analysis.

4.1.2. Vegetation sampling

As mentioned earlier, a 10 m. radius circular plot was laid at every 200 m. interval, along the line transects. Apart from pellet counts, this was also used for vegetation sampling. In all, there were 99 such sampling stations. Within each 10 m. radius circular plot, the following parameters were measured:

i) Tree density: woody species exceeding 20 cm. in GBH (Girth at Breast Height) were considered as trees. Even if a tree was partially inside the limits of the plot, in was counted as being 'in'.

ii) Tree GBH: which was measured to the nearest centimetre for all trees inside the plot.

iii) Tree height: which was estimated visually. Later, in order to test the reliability of the visual estimates, an exercise of measuring heights of 20 trees was carried out. Visual estimates were reliable. **(Appendix II).**

iv) Canopy cover: this was measured using a rear view mirror with grids, for four points within the plot. This was done twice in winter and once in summer season. Later, to assess the reliability of this approach, it was compared against a GRS Densiometer. It was found that the grid mirror approach was reliable. **(Appendix III)**.

v) Leaf stage of the trees: the young to mature leaf stages of leaves were scored on a 5-point scale: 0 (no leaves), 1 (fully mature), 2 (partly mature), 3 (equal young and mature) and 4 (mostly young leaves). This was done twice in winter and once in summer.

vi) Greenness of leaves: the greenness of foliage was again scored on a 5-point scale, 0 (all dry), 1 (1/4th green), 2 (half-green), 3 (3/4th green) and 4 (all green). This was done twice in winter and once in summer. This was done twice in winter and once in summer.

vii) Ground cover: based on Point Intercept Method (Mueller-Dombois and Ellenberg, 1974). 50 points at 20 cm. intervals along a 10 m. long measuring tape were noted down. Every point was grouped into one of the following: Bare soil, Rock, Litter, Grass (with its species and colour, i.e. green, yellow, or brown) and Herb (with species). This was done twice in winter and once in summer.

viii) Litter weight: using a 25 cm. X 25 cm. quadrat frame at four points in the plot, the weight of palatable litter material was measured. Inedible and unpalatable substances like twigs and dirt were removed before weighing. From literature, fallen leaves of *Anogeissus* and *Zizyphus*, fruits of *Acacia* and *Zizyphus* were known to be palatable for the study species. Weights were taken to the nearest gram using a spring balance (Pesola, *100 gm.*). This was done twice in winter and once in summer.

At the same sampling point, within the 10 m. radius plot, a 5 m. radius nested circular plot was laid to measure the following parameters –

i) Shrub density: all shrub species and woody species below 20 cm. in GBH were counted. Even if a particular plant was partially inside the limits, it was considered 'in'.

ii) Shrub height: the maximum height of each shrub was measured to the nearest centimetre.

iii) Leaf stage: similar as in the case of the trees, young to mature leaf stages of leaves was scored on a 5-point scale: ranging from 0 (no leaves), 1 (fully mature), 2 (partly mature), 3 (equal young and mature) and 4 (mostly young leaves). This was done twice in winter and once in summer.

iv) Greenness: similar to the case of trees, the greenness of foliage was again scored on a 5-point scale, ranging from 0 (all dry), 1 (1/4th green), 2 (half-green), 3 ($3/4^{th}$ green) and 4 (all green). This was done twice in winter and once in summer.

Apart from vegetation parameters, certain other aspects were also measured in the 10 m. radius circular plot:

i) Slope: measured using a map-reading compass-cum-clinometer (SILVA type 15). Readings were taken at four points inside the plot, by laying the equipment on the ground, directed along the slope.

ii) Distance to water: estimated by using 1:50,000 scale Survey of India toposheets. Based on this, the distance between a plot and the nearest water source was put into 500 m. class intervals. This was done once in winter and once in summer.

4.1.3. Food habits

Fresh fecal samples of the study animals were collected opportunistically for studying their food habits and were sun dried. Later they were dried in an oven at 60° C. for 48 hours. Identification of species from pellets was done instantly by observing shape and size characteristics of the pellets (**Appendix I**). Food habits were determined according to the following procedure:

i) 20 pellet groups were collected for each species in a season, from various parts of the study area. After drying, two pellets from each were taken to form a composite sample. Two such composite samples were made for each species for each season.

ii) Following Holechek (1982), each of the composite pellet samples were ground by a grinder (*Tecator* grinding mill) to 1 micron size, treated with Hertwig's solution and then mounted on glass slides using Hoyer's solution. These slides were observed under a compound microscope for identification of undigested fragments. From each sample, three slides were prepared for observations. Every identifiable fragment was put as either 'grass' or 'browse' based on venation patterns (Stewart, 1967).

iii) Initially, 50 fragments were examined in each slide to calculate sample size requirements. Then, sample size was determined based on the stabilization of grass-to-browse ratio, using graphical assessment.

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4.2. Data Analysis

4.2.1. Estimating population size and relative abundance of study species

Line transect sampling methods (Anderson *et al.,* 1979) is one of the best ways of estimating animal populations. This method uses probability of detecting animal clusters away from the transect line to construct a Probability Density Function (PDF) (Burnham *et al.*, 1980). Depending on the shape of the PDF, different models are chosen among Uniform, Half-Normal, Fourier series and Negative exponential types of distributions; to arrive at a "best fit". The goodness of the "fit" is judged by a likelihood measure, the Akaike Information Criteria (AIC). The programme DISTANCE (Laake *et al.,* 1994) was used to carry out this procedure for density estimation. Densities of all four species were calculated in this manner. from the data collected in winter and summer seasons. But, because of low sample size, the estimates for chinkara were done by pooling both seasons together.

4.2.2. Characterization of different habitat types

Eleven sites recognized in the study area were based on their local names and broad vegetation features. Each site was a unit of sampling, through which line transects passed and vegetation plots had been laid. These 11 sites were subjected to a Cluster Analysis procedure (Pielou, 1984) in order to judge similarities between them. Terrain and vegetation parameters provided the data for this analysis, such as- tree density (median number of trees in plots), number of tree species (median number of tree species in plots), shrub density (median number of shrubs in plots), number of shrub species (median number of shrub species in plots) and canopy cover (median canopy cover in the plots). Median as a measure of central tendency is less influenced by extreme values and hence was chosen over other measures. Hierarchical divisive algorithm was carried out using the software SPSS for Windows (8.0) (Norussis, 1990) with between-group linkages and Euclidean distance measures.

4.2.3. Investigating macro-level Resource selection

Broad scale selection occurs when animals choose between different habitat types (Rosenzweig 1981). So selection between different habitat types by each of the four study species was investigated by using the indirect evidences in the form of dung/pellet deposition. Dung/pellet count is widely used and a good indicator of overall habitat selection because it reveals habitat use by animals over a 24-hour period (Rogers *et al.*, 1958; Neff, 1968; Cairns and Telfer, 1980). Direct sightings from transect walks are restricted in time, and thus were not used for the analysis of resource selection in the present study. A comparison-of-mean exercise, based on the rate of pellet deposition in plots of different habitat types, can provide insight into this matter.

Because of unequal number of days for deposition, all pellet counts had been standardized for 100 days. These standardized counts of each of the four species were compared between the plots in different habitat types. Frequent zero scores meant that the pellet count data belonged to a distribution other than normal. In fact, it is expected that pellet-count data pertain to negative-binomial rather than normal distribution (White and Eberhardt, 1980). So, a distribution free test, Kruskal-Wallis ANOVA (Zar, 1984) was carried out to compare the different habitat types. Following this, a distribution free multiple comparisons of means were carried out using the software *KyPlot* version 2.0 (Yoshioka, 1999).

4.2.4. Investigating into micro-level Resource selection

As pointed out earlier, indirect evidence in the form of deposited pellets, serves as a better indicator of habitat use than the temporally constrained direct observations. Thus, like in the case of broad level selection, the data on pellet counts were used to explore micro-level resource selection as well. Each vegetation plot had provided information on the following variables: tree density, number of tree species, median GBH for a plot, median tree height, median score for tree leaf stage, median score for tree greenness, shrub density, median shrub height, median scores for shrub leaf stage, median score for shrub greenness, median number of shrub species, median canopy cover, median grass cover, median rockiness, median barrenness, median litter cover on ground, median slope and the mean weight of palatable litter material. In addition, data on the distance to water; scored as 1 to 4 (for 500 m. classes) for each plot had been collected. A derived variable, representing woody stem cover, was constructed in the form of sum of all GBH values in a plot. To reduce the dimensionality of this data, the data matrix was subjected to ordination using Principal Component Analysis (PCA) method of Factor Analysis in SPSS for Windows (8.0) (Norussis, 1990). Ordination by correlation matrix was used because the variables were measured in different units.

Ordination and allied multivariate techniques require the data to fulfill certain assumptions. Most important for PCA are: a). Multivariate normal distribution and b). Homogeneity of variances. There are no easy methods for testing for multivariate normal distribution and the tests for homogeneity of variances are unreliable if data are not multivariate normal. In view of this double problem it was decided to run PCA with z-transformed variables. Thus, all the variables were z-transformed and a parallel PCA procedure was carried out in addition to the one using raw data.

Use of predictive models by logistic regression analysis, to elaborate habitat selection has been shown to be useful in several taxa (Franco *et al.*, 2000; Johnson *et al.*, 2000). Trexler and Travis (1993) have discussed this approach along side other traditional parametric procedures. As the pellet count data did not belong to normal distribution, they were converted into binary form i.e. presence or absence of pellets of particular species in each plot. With this binary information, a probabilistic model was constructed using Principal Component (PC) scores alongside the presence/absence of livestock dung for all 99 plots. This was done by evaluating the PC scores and presence/absence of livestock dung as independent variables in a logistic regression analysis with binary response in the form of presence/absence of pellets of species. In this manner, key factors that influence use of certain areas by individual species. This logistic regression model was constructed with data for each season, using PC scores from raw data as well as z-transformed data. This was done to check whether the results were robust towards violations of assumptions of multivariate data analysis. Based on the correctness of classification of used and unused sites, a measure for proportional change in error was constructed for the model. This construction was based on the following formula (Menard, 1995):

$$\boxed{\Phi = [\{(a+b)(b+d)/N\} + \{(c+d)(a+c)/N\} - (b+c)]/\ [\{(a+b)(b+d)/N\} + \{(c+d)(a+c)/N\}]}$$

where Φ = Proportional change in error (PE), N = sample size and a, b, c, d, are classes in the contingency tables of the following form:

a	b
c	d

Later, in order to validate the model, it was reconstructed using only a subset of the original data (3/4th of the total data points) and tested over the remaining subset (remaining 1/4th).

4.2.5. Examining food habits

Diet of the study species was examined in terms of grass: browse ratio found by microhistological analysis of their pellets. This enabled in placing the four species along the *grazer-browser continuum.* Based on this information on diet composition of each species, a dissimilarity matrix was prepared from the grass-browse ratios for each season. This was done using *XLSTAT* (Fahmy, 2001) matrix operation procedures in MS Excel (Windows 98). This matrix was used in conjecture with other matrices in further analysis.

4.2.6. Means of resource partitioning

Study animals were known to be most active in foraging during early and late hours of the day (Chakrabarty, 1991) and direct evidence form transect walks were obtained during the same time. Since foraging is the most important of all consumptive uses, this information was considered for the analysis of resource partitioning. The sighting of a particular species during all transect walks in winter and summer were taken as the dependent variable. The independent ones were the z-transformed variables that had been used during PCA.

Discriminant Analysis was used to investigate the segregation among species in terms of resource utilization. First step in Discriminant Analysis was to check whether the centroids of utilized resources differed between the four species. This is equivalent to testing a multi-sample hypothesis of equality of means in univariate format. But since all the resource states formed a multi-dimensional state, comparison of centroids was carried out. Program S-PLUS 2000 (S-PLUS. Mathsoft Inc.) was used to determine differences in the group centroids. Following this multi-sample test, a multiple-comparison test was carried out to see differences between individual species.

Once the multi-sample as well as pair-wise contrast tests were over, an attempt for determining key factors that help in separating the four species were carried out. Discriminant Functions were extracted from the various independent variables using stepwise method in SPSS for Windows (8.0) (Norussis, 1990). The criterion for this procedure was set towards maximization of the Mahalanobis distance between the four species cenroids. This approach has been shown to be appropriate for such purposes (Edge *et al.*, 1987). Based on the Discriminant Function scores, graphical evaluation of spatial overlap between species was done. The distances between centroids of species clusters (Mahalanobis distance) were used to obtain a dissimilarity matrix for both seasons (Venables and Ripley, 1994). The matrix of Mahalanobis distance represented species separation in space. The dissimilarity matrix constructed from diet analysis represented the same in the corresponding dimension of food. Ecological separation must be addressed with simultaneous assessment of these two aspects. Non-metric multi-dimensional scaling (Spence, 1978) was used to combine these two types of matrices. This procedure was carried out using SPSS for Windows (8.0) (Norussis, 1990) and a composite idea of the niche relationships of the study species was obtained.

Several variables related to vegetation, terrain and other features, measured at the sampling plots over the two seasons were used for analysis purpose. Table 1. describes these variables in context of the present study.

Table 1. Descriptive statistics of the variables used for Principal Components Analysis (PCA)

	Variable	Winter		Summer	
		Mean	SD	Mean	SD
Tree variables	No. of Trees per plot	12.56	9.79	-	-
	GBH (Median)	57.71	25.59	-	-
	Sum of all GBH per plot	645.08	406.32	-	-
	Tree height (Median)	7.21	2.33	-	-
	Leaf stage of Trees	0.97	0.17	1.03	0.30
	Greenness of Trees	1.04	1.21	0.47	0.90
	Canopy cover (Median)	18.94	16.02	-	-
Shrub variables	No. of Shrubs (Median)	8.47	7.30	-	-
	Shrub height (Median)	87.40	82.17	-	-
	Leaf stage of Shrubs	0.89	0.40	1.06	0.64
	Greenness of Shrubs	1.35	1.34	0.83	1.28
	No. of Shrub species (Median)	1.88	1.31	-	-
Ground cover	Grass cover (Median)	7.30	10.07	-	-
	Litter cover (Median)	20.45	13.22	16.84	11.95
	Rockiness(Median)	9.24	6.60	-	-
	Barrenness(Median)	12.64	10.63	-	-
Others	Litter weight (Median)	5.32	4.20	4.42	3.81
	Slope (Median)	5.78	6.80	-	-
	Distance to water	2.30	0.89	2.17	0.8

5. Results

5.1. Population estimates of study species

Sample sizes permitted densities to be calculated by the program DISTANCE according to seasons for chital, sambar and nilgai, but not for chinkara. Therefore, data for both seasons had to be pooled in the latter case.

Based on group densities and group sizes, densities in terms of number of individuals were calculated.

In winter, chital was found to be most abundant of the four species (33.44 animals/sq.km., %C.V=40.27), followed by sambar (20.54 animals/sq.km., %C.V=34.84) and nilgai (13.12 animals/sq.km., %C.V=41.58). In summer, chital was again the most abundant species (24.85 animals/sq.km., %C.V=41.37), followed by sambar (14.44 animals/sq.km., %C.V=39.48) and nilgai (11.08 animals/sq.km., %C.V=38.10). Chinkara was the least abundant of the four species with densities of 5.61 animals/sq.km. (%C.V=31.97) (Table 2.). It appeared that animal densities dropped from winter to summer (Fig. 3). There was an overall decline of 15% to 30% in the density of chital, sambar and nilgai across the seasons.

Table 2. Density estimates of four species in the study area in two seasons in Ranthambhore National Park, Rajasthan

Season	Species	Sample size	Model	Adjustment	Density (no./sq.km)	CV(%)
Winter	Chital	146	Half-Normal	Cosine	33.44	40.27
	Sambar	122	Uniform	Cosine	20.54	34.89
	Nilgai	111	Hazard-Rate	Cosine	13.12	41.58
Summer	Chital	110	Uniform	Cosine	24.85	41.37
	Sambar	76	Hazard-Rate	Cosine	14.44	39.48
	Nilgai	79	Uniform	Cosine	11.08	38.10
Pooled	Chinkara	52	Hazard-Rate	Cosine	5.61	31.97

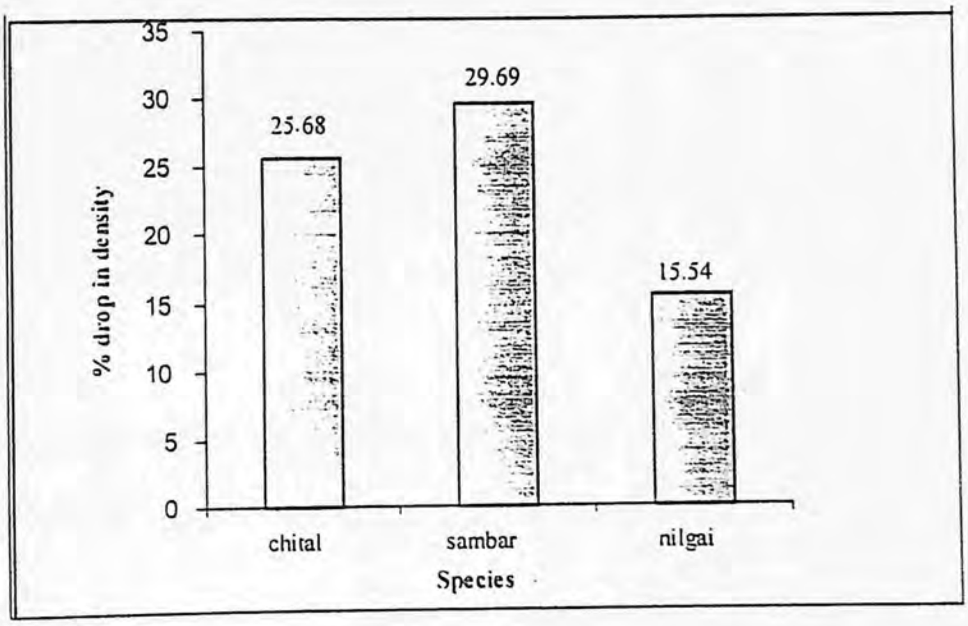


Figure 3. Drop in estimated densities of three species across two seasons (winter and summer), in Ranthambhore National Park, Rajasthan.

5.2. Habitat classification

Cluster Analysis run on the eleven sites in the ISA gave rise to five distinct groups. These five groups were significant as they could be easily interpreted in ecological terms. These groups were:

- Habitat A: *Anogeissus pendula* forest with *Grewia flavescens* in the shrub layer. This had around 452 trees/ha and 830 shrubs/ha on an average with 65% and above canopy cover.
- Habitat B: *Anogeissus* mixed with *Capparis-Dichrostachys* scrub. Here 522 trees and 1660 shrubs occurred in a hectare on an average. Canopy cover touched 50%.
- Habitat C: *Anogeissus-Diospyros* forest with dwarf shrub layer. Around 910 trees and about than 730 shrubs (usually <0.5 m. in height) were to be found in a hectare, with canopy cover exceeding 75% on average.
- Habitat D: *Anogeissus-Acacia-Zizyphus-Butea* mixed woodlands. About 200 trees and around 920 shrubs would be found in a hectare of this habitat; canopy cover would be around 20%.
- Habitat E: Grassy slopes and plateaus with sparse tree cover. Sparse tree cover (around 115 trees/ha) and shrub cover (around 230 shrubs/ha) without any canopy characterized this habitat.

The dendrogram (Fig. 4) shows these five habitat types. Since these five groups were ecologically meaningful, they were considered as five separate sub-units in the space dimension, to understand spatial resource by the study species. Coarse scale resource selection (macro-level) was looked at in terms of these habitat types.

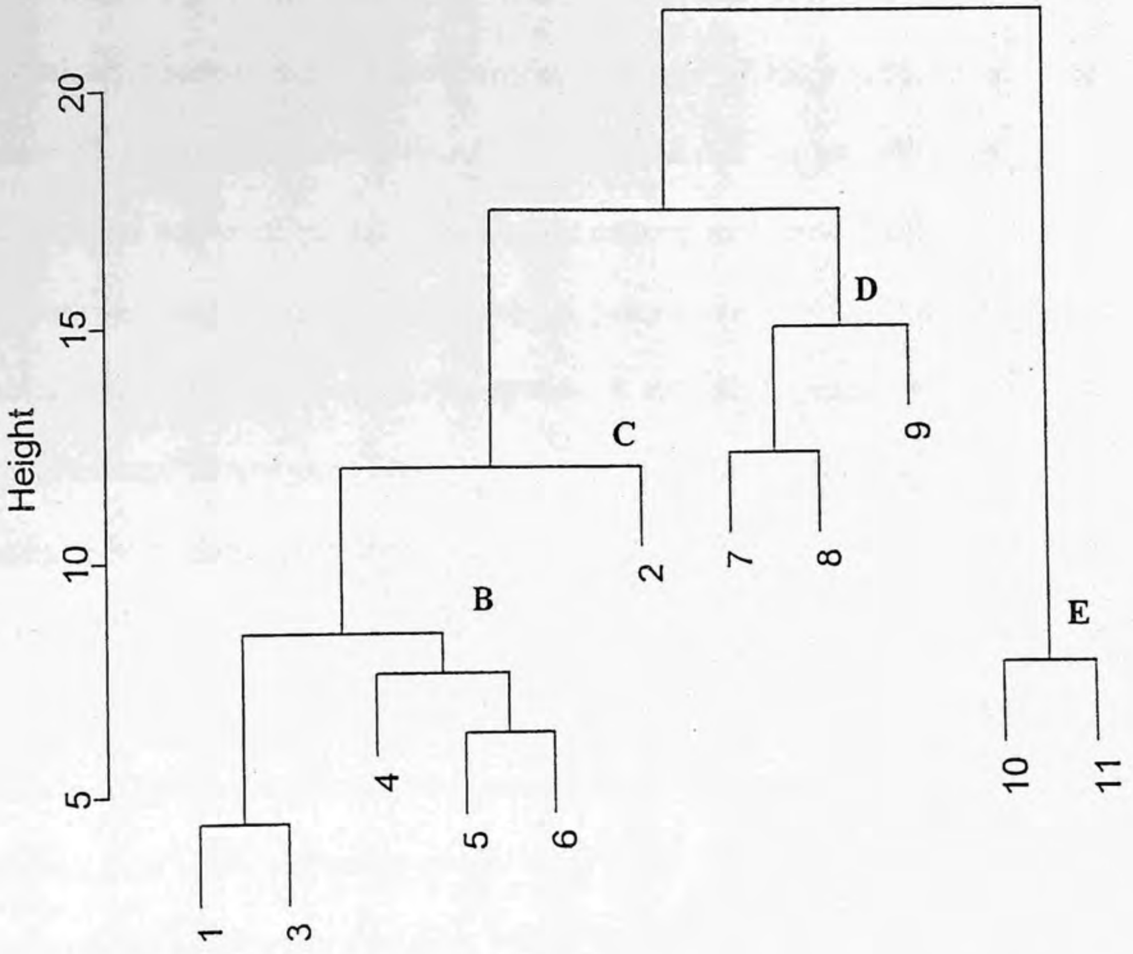


Fig. 4: Dendrogram of eleven sites in the Intensive Study Area showing the formation of five Habitat types.

Description of Habitat types
Type A: (1+3) = *Anogeissus* forest with *Grewia*
Type B: (4+5+6) = *Anogeissus* forest with *Capparis-Dichrostachys* scrub
Type C: (2) = *Anogeissus-Diospyros* forest with dwarf shrub layer
Type D: (7+8+9) = *Acacia-Zizyphus-Anogeissus* woodland
Type E: (10+11) = Grassy slopes and plateaus

5.3. Macro-level resource selection

The rate of pellet deposition, as an indicator of intensity of habitat use was compared for each species across the five habitat types for both seasons. Kruskal-Wallis one-way ANOVA was employed to test for equality of means as data on pellet deposition did not belong to the normal distribution (Kolmogorov-Smirnov goodness of fit, $p<0.05$ for all species in each season; Table 3). Kruskal-Wallis ANOVA showed that the rate of deposition of pellets by each species across all habitat types was not uniform in each season ($p<0.01$ for each species for both seasons), (Table 4). In ecological perspective, this suggested towards differential habitat selection by each of the four species. A multiple comparison test showed patterns in the differential habitat use (Table 5). Habitat C (*Anogeissus* forest with scanty shrub cover) seems to be responsible for rejection of the null hypothesis in chital. Habitat type E (Grassy slopes and plateaus) possibly caused rejection in case of sambar. Seemingly, the hypothesis got rejected for nilgai due to Habitat E. For chinkara, the hypothesis seems to be rejected because of Habitat A (*Anogeissus-Grewia*). This argument is supported by the mean ranks assigned to the habitat types by the Kruskal-Wallis test (Table 6). Habitat C had received a high rank for chital while in sambar habitat E had a very low rank. For nilgai, habitat E had high rank while it was habitat A in case of chinkara. This trend was consistent across the seasons.

Table 3. Kolmogorov-Smirnov test for normality of rate of pellet deposition across two seasons by four species in Ranthambhore National Park, Rajasthan

	Chital		**Sambar**		**Nilgai**		**Chinkara**	
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
Mean	19.25	25.01	13.30	12.04	6.19	6.11	1.00	1.27
SD	31.28	32.58	18.83	15.55	9.59	9.16	2.22	2.44
Z	2.67	2.20	2.38	2.18	2.57	2.51	3.90	3.84
Sig.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4. Kruskall-Wallis ANOVA on rate of dung deposition across five Habitat types for two seasons in Ranthambhore National Park, Rajasthan

	Chital		**Sambar**		**Nilgai**		**Chinkara**	
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
Chi-square	22.751	17.149	61.723	13.894	62.630	44.041	24.639	50.177
df	4	4	4	4	4	4	4	4
Sig.	.000	.002	.000	.008	.000	.000	.000	.000

Table 5. Results of Tukey's HSD-equivalent Steel-Dwass test for multiple comparisons of five habitat types for rate of dung deposition by four species.

Species	Chital		Sambar		Nilgai		Chinkara	
Habitat-pair[$]	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
A-B	-	-	**	-	**	**	**	**
A-C	*	-	-	*	-	-	-	-
A-D	-	-	-	-	-	-	-	-
A-E	-	-	**	-	**	**	-	*
B-C	**	**	**	*	-	-	**	-
B-D	-	-	**	-	**	**	**	**
B-E	**	-	-	-	-	-	-	-
C-D	**	**	-	*	-	-	-	-
C-E	-	**	**	*	**	**	*	**
D-E	-	-	**	-	**	**	-	-

* difference was significant at 0.05 level of confidence.

** difference was significant at 0.01 level of confidence

\- denote that the difference was not significant at 0.05 level

$ Habitat A: *Anogeissus-Grewia* forest
Habitat B: *Anogeissus-Dichrostachys-Capparis* mixed scrub
Habitat C: *Anogeissus-Diospyros* with dwarf shrub cover
Habitat D: *Acacia-Zizyphus-Anogeissus* woodland
Habitat E: Grassy slopes and plateaus

Table 6. Mean ranks in Kruskall-Wallis ANOVA for pellet deposition across five habitat types in two seasons by four species in Ranthambhore National Park, Rajasthan

Species	Habitat	Sample size	Mean Rank	
			Winter	Summer
Chital	A	9	53.72	49.67
	B	36	61.06	57.65
	C	10	20.00	18.00
	D	28	53.95	54.89
	E	16	34.88	44.41
Sambar	A	9	29.39	48.83
	B	36	71.43	55.46
	C	10	20.50	21.50
	D	28	28.71	48.38
	E	16	69.06	59.03
Nilgai	A	9	81.39	81.28
	B	36	33.03	38.57
	C	10	74.45	60.95
	D	28	68.71	66.11
	E	16	22.50	23.09
Chinkara	A	9	67.72	76.61
	B	36	38.17	35.47
	C	10	61.60	86.20
	D	28	59.05	51.34
	E	16	43.56	42.75

5.4. Micro-level resource selection

The Principal Component Analysis of habitat variables collected from the vegetation plots gave five Principal Components (PC) in each season. The selection of PCs was based on Kaiser-Guttman Criteria (Jackson, 1993). These five PCs could explain 74.6% of the original variation in winter and 71.4% in summer (Table 7). The Kaiser-Meyer–Olkin measure was 0.625 in winter and 0.644 in summer. Bartlett's test of sphericity suggested that neither in winter nor in summer were the data forming identity matrices ($p<0.05$ in both seasons).

When the z-transformed variables were used to construct PCs, the outcome was almost identical to that from raw variables, in both seasons (Table 7). All PCs could be interpreted in ecological contexts. Ecological meaning for PCs created from raw variables and z-transformed variables were not much different.

In winter, the PCs had following interpretation:

- PC 1: Represented sites with high tree density (i.e. > 900 trees/ha). The sum of GBH was high in these plots and so was the canopy cover. Thick *Anogeissus-Diospyros* forest with dwarf shrub layer (less than 0.5 m. high) were represented in this PC.
- PC 2: Represented sites with high shrub cover in flat terrain (around 1000 shrubs/ha). The score for shrub greenery was high. So, sites with *Capparis sepiaria* and *Balanites aegyptica* and other evergreen shrubs were represented by this factor.
- PC 3: This factor was more or less similar to PC 2 in ecological sense, representing mixed scrubland sites.
- PC 4: This factor was related to thick trees (i.e. GBH above 100 cm.), which had green leaves. Thus, this PC represented *Acacia-Zizyphus-Anogeissus* woodland with *Butea monosperma*.
- PC 5: This factor was related to well-wooded areas (around 400 trees/ha) close to water (i.e. within 1 km. from water). It represented pure stands of *Anogeissus* forest in the vicinity of the permanent water bodies.

In summer season, the interpretation of the factors were like the following:

- PC 1: Areas of thick *Anogeissus* forest with little shrub cover.

- PC 2: Scrubland with *Capparis* and other evergreen species.
- PC 3: *Acacia-Zizyphus-Butea* type of woodland.
- PC 4: *Anogeissus* forest with *Grewia* on the slopes.
- PC 5: Areas with tall shrubs (i.e. forests with *Grewia*), but close to water.

A predictive model was constructed when binary response variable in the form of presence/absence of pellet groups of a particular species was used for logistic regression analysis. The inclusion of variables in the model was done by the principle of parsimony. Menard (1995) has recommended inclusion of all variables prior to their 'Backward Elimination'. He has also suggested a relaxation of the α level to 0.15 for such a procedure. But for this analysis, significance was considered at $p<0.1$ and results are shown for the most parsimonious model, with variables having significance of $p< 0.1$. Sites used by all species could be classified correctly by the model with accuracy ranging from 58.62% (chinkara in summer) to 90.91% (nilgai in winter). But overall PE ϕ were not remarkably high (from 0.28 for sambar in summer to 0.73 for nilgai in summer). This reduction in PE ϕ was mainly due to misclassifications in the unused sites. The results of this predictive model are summarized in Table 8.

This predictive model was tested for its efficiency. Validation of $1/4^{th}$ of the data set suggested that the model was quite efficient. Most of the used sites were correctly classified for each species (chital, 58% in winter and 80% in summer; sambar, 85% in winter and 55% in summer; nilgai, 82% in winter and 86% in summer; chinkara, 100% in winter and 66% in summer). However, correct classifications of unused sites were not remarkably high. This resulted in moderate PE ϕ scores (Table 9).

Table 7. Summary of Principal Components (PCs) extracted by PCA on raw and z-transformed variables of two seasons

A) Winter

Factor	Variables		Eigen Values		% variance		Cumulative % variance	
	Raw variable	Z-transformed.	Raw	Z-tr.	Raw	Z-tr.	Raw	Z-tr.
PC 1	Tree no. GBH sum Canopy	Tree no. GBH sum Canopy	4.84	4.84	28.50	28.50	28.50	28.50
PC 2	Bare Slope* Shrub greenness	Bare Slope* Shrub greenness	2.40	2.39	14.11	14.11	42.62	42.62
PC 3	No. of shrubs Shrub leaf stage No. of shrub species	No. of shrubs Shrub leaf stage No. of shrub species	2.16	2.16	12.75	12.75	55.37	55.37
PC 4	GBH Tree leaf stage	GBH Tree leaf stage	1.89	1.89	11.16	11.16	66.54	66.54
PC 5	Distance to Water Tree greenness*	Distance to Water Tree greenness*	1.37	1.37	8.07	8.07	74.62	74.62

B) Summer

Factor	Variables		Eigen Values		% variance		Cumulative % variance	
	Raw	Z-tr.	Raw	Z-tr.	Raw	Z-tr.	Raw	Z-tr.
PC 1	No. of Trees GBH sum Canopy	No. of Trees GBH sum Canopy	4.97	4.97	26.18	26.18	26.18	26.18
PC 2	Shrub leaf stage Greenness of shrubs Barrenness	Shrub leaf stage Greenness of shrubs Barrenness	3.21	3.21	16.92	16.91	43.10	43.10
PC 3	Tree leaf stage Greenness of trees	Tree leaf stage Greenness of trees	2.30	2.30	12.11	12.11	55.21	55.21
PC 4	No. of shrubs Slope	No. of shrubs Slope	1.55	1.55	8.19	8.20	63.41	63.42
PC 5	Distance to water Shrub height	Distance to water Shrub height	1.51	1.51	7.99	7.99	71.40	71.41

* indicates negative loading

Table 8. Summary of logistic regression model of Habitat selection by four species in Ranthambhore National Park, Rajasthan

	Variable	Co-efficient	S.E of co-efficient	% accuracy for presence	PE ϕ
Chital	PC 2	-0.5847	0.23	90%	0.38
	PC 5	1.7024	0.74		
	Cattle	-0.2078	0.35		
Sambar	PC 2	-3.5718	0.74	88.14%	0.68
	PC 5	-0.7946	0.34		
	Constant	0.7172	0.36		
Nilgai	PC 1	1.9988	0.53	90.91%	0.71
	Cattle	6.0445	1.2		
	Constant	-2.0498	0.59		
Chinkara	PC 1	2.0186	0.64	72.41%	0.65
	PC 2	3.7692	0.90		
	Constant	-2.8477	0.72		

A) Winter

	Variable	Co-efficient	S.E of co-efficient	% accuracy for presence	PE ϕ
Chital	PC 2	-0.8460	0.25	85.94%	0.37
	PC 5	-8942	0.27		
Sambar	PC 3	0.5341	0.25	84.21%	0.28
	PC 5	-0.3694	0.22		
	Constant	0.3349	0.21		
Nilgai	PC 1	1.3842	0.35	87.72%	0.73
	PC 3	0.9472	0.43		
	Cattle	3.9522	0.85		
Chinkara	PC 2	1.3059	0.31	58.62%	0.53
	PC 4	-1.5209	0.43		
	Constant	-1.4195	0.33		

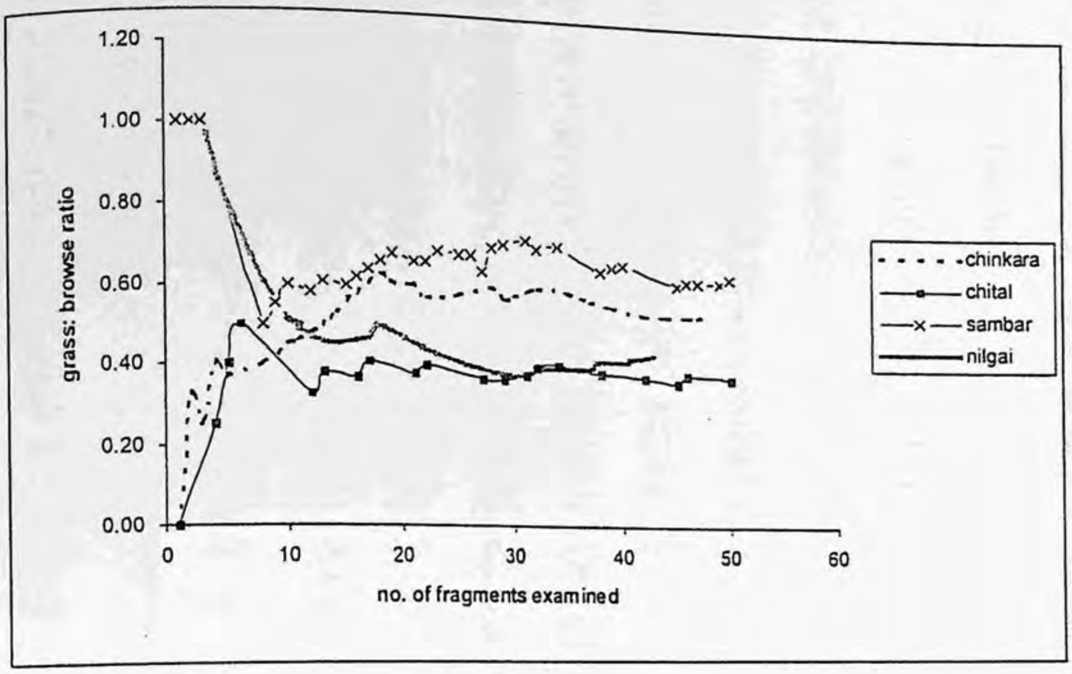
B) Summer

Table 9. Performance of logistic regression model after validation to predict habitat use by four species across two seasons in Ranthambhore National Park, Rajasthan

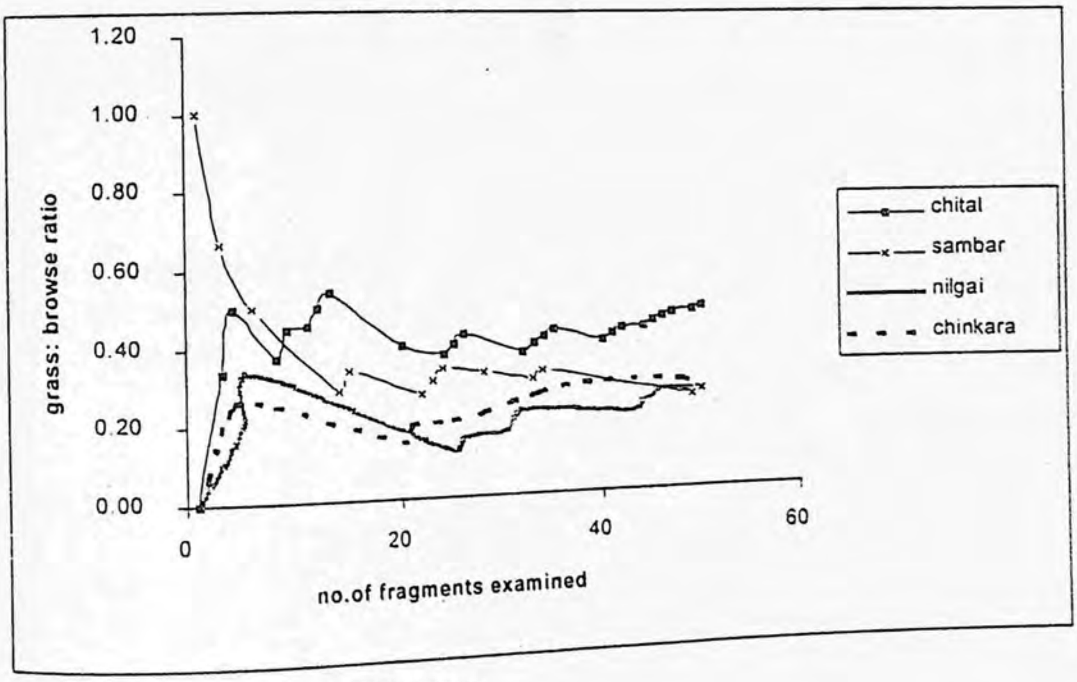
Species	% correct for presence		% correct for absence		`PE ϕ	
	Winter	Summer	Winter	Summer	Winter	Summer
Chital	58	80	50	50	0.14	0.26
Sambar	85	55	100	71	0.83	0.14
Nilgai	82	86	73	20	0.63	0.66
Chinkara	100	66	88	73	0.81	0.27

5.5 Food habits

Results indicated that the grass: browse ratio stabilized after examination of around 30 to 35 fragments in the slide preparations for all the four species. This trend was consistent across seasons (Fig. 5). Thus examining 50 fragments provided adequate sample size for the purpose. Higher values (>1) of the grass: browse ratio indicated greater contribution of grass in the diet of the animal. Chital used little grass in winter (grass: browse ratio 0.53) while sambar was consuming considerable grass (grass: browse ratio 1.03). Nilgai (grass: browse ratio 0.63) was dependent on browse, whereas chinkara was substantially dependent on grass (grass: browse ratio 0.91). The diet composition in form of grass: browse ratio changed across seasons for all species (Fig. 6). All species showed a decline in utilization of grasses during summer. The grass: browse ratios were: chital, 0.4; sambar 0.5, nilgai 0.38 and for chinkara 0.35. A Cluster Analysis procedure run over the dissimilarity matrices calculated from grass-browse ratio (Table 10), showed three distinct groups in terms of diet in each season. In winter, sambar and chinkara occupied distinct positions while nilgai and chital showed close affinities in diet (Fig. 7A). In summer, the same trend was maintained, with sambar and chinkara far apart from the closely associated pair of nilgai and chital (Fig. 8A).



A) Winter



B) Summer

Fig. 5. The change in grass: browse ratio with sample size, in the diet of four species of ungulates in Ranthambhore National Park, Rajasthan.

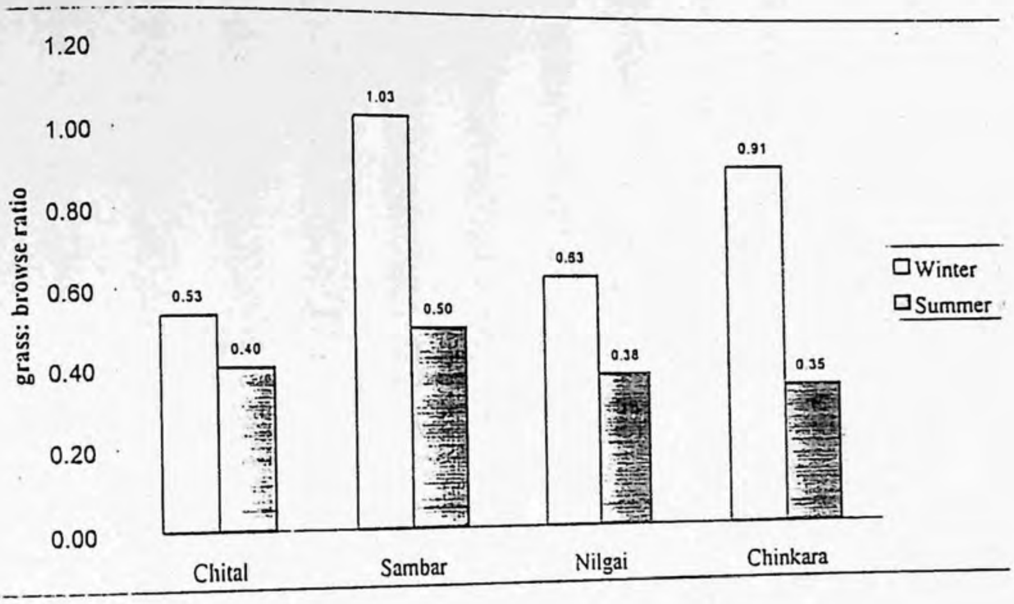


Fig. 6: Change in diet composition (grass: browse ratio) across two seasons (winter and summer), of four ungulate species in Ranthambhore National Park, Rajasthan.

Table 10. Matrix of Euclidean distance measures between species based on dissimilarity in diet

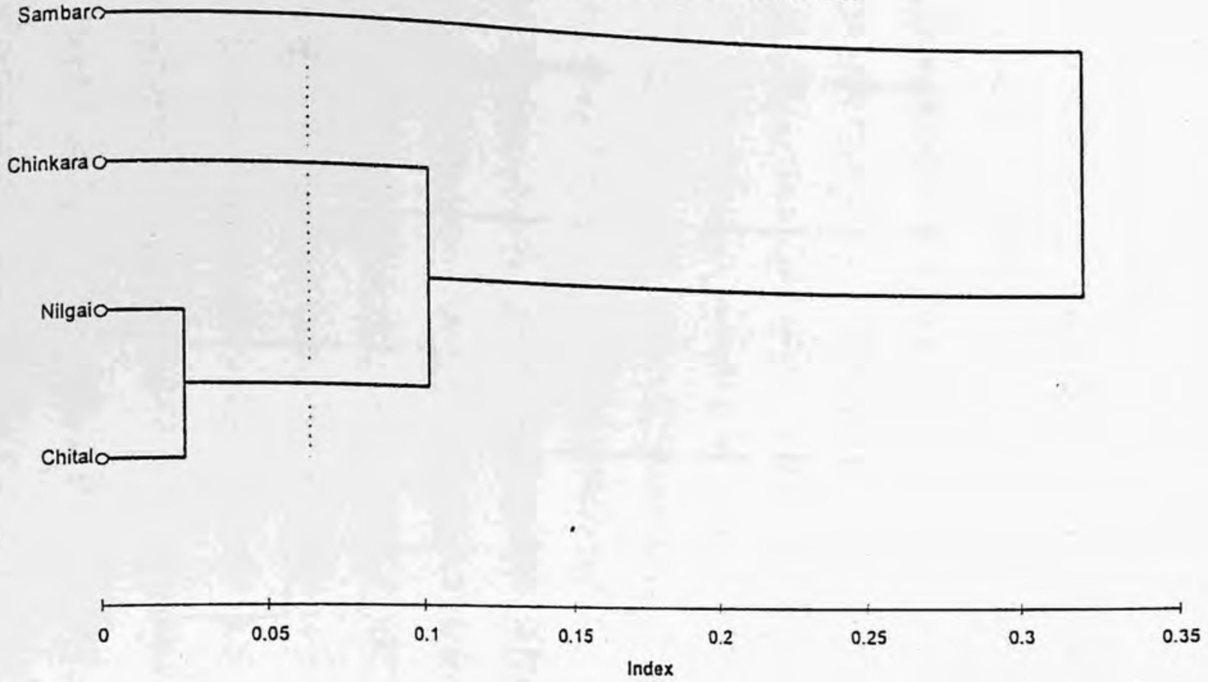
Species	Chital	Sambar	Nilgai	Chinkara
Chital	0	1.10	0.10	0.38
Sambar	-	0	1.00	0.72
Nilgai	-	-	0	0.28
Chinkara	-	-	-	0

A) Winter

Species	Chital	Sambar	Nilgai	Chinkara
Chital	0	0.10	0.02	0.05
Sambar	-	0	0.12	0.15
Nilgai	-	-	0	0.03
Chinkara	-	-	-	0

B) Summer

A) Dendrogram of dissimilarity in use of food resources



B) Dendrogram of dissimilarity in use of spatial resources

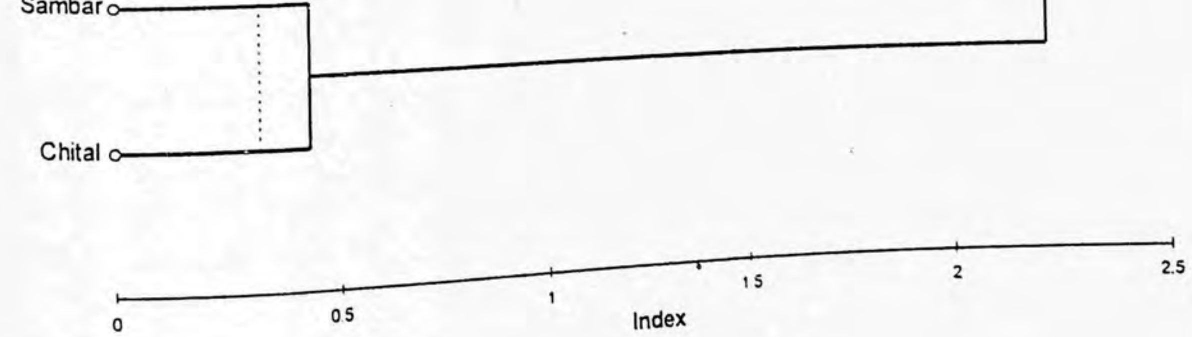
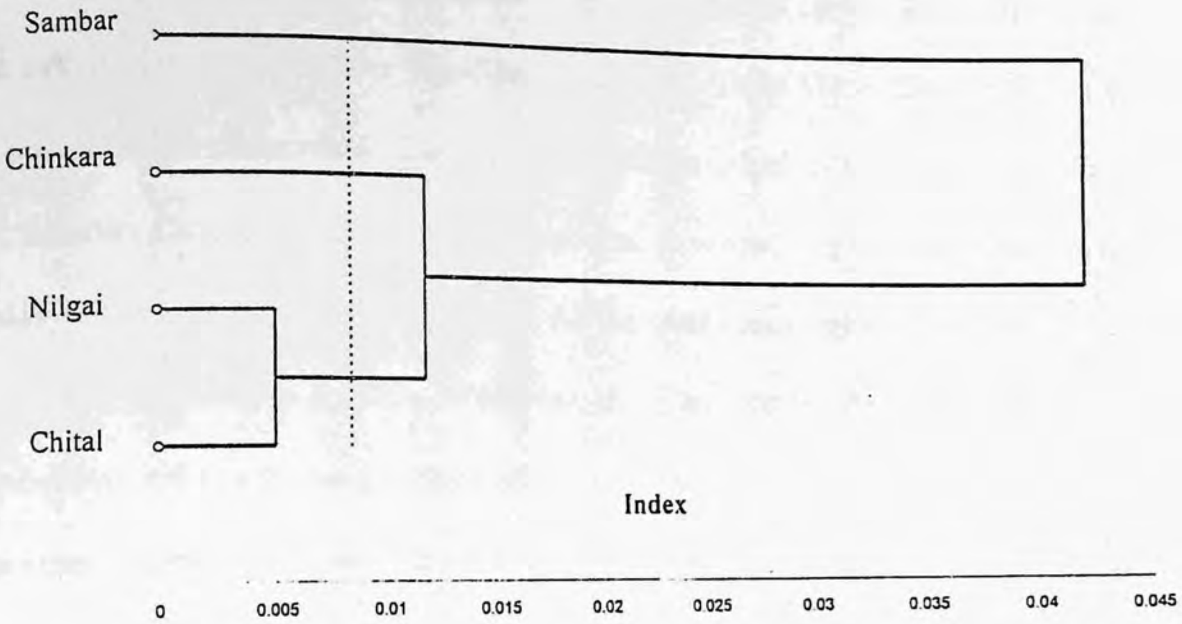


Fig. 7: Dendrogram showing dissimilarity in use of spatial and food resources between four species during Winter season in Ranthambhore National Park


A) Dendrogram showing dissimilarity in use of food resources

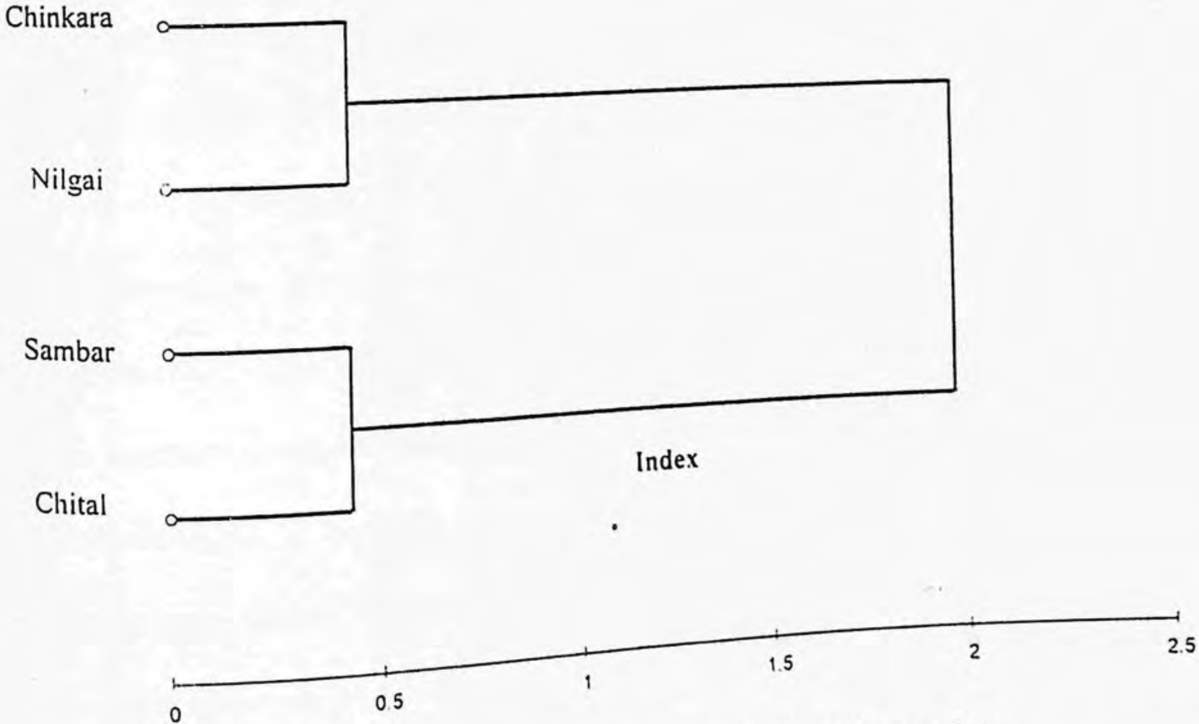

B) Dendrogram showing dissimilarity in use of spatial resources

Fig. 8: Dendrograms showing dissimilarities between four species in use of spatial and food resources during Summer

5.6 Means of Resource Partitioning

Preliminary Discriminant Analysis by a procedure analogous to a Multivariate Analysis of Variance (MANOVA) (Scheiner, 1993), suggested that centroids of species' utilization were different from each other in both seasons. The test statistic of choice, Pillai's Trace indicated that the species centroids were significantly different, (Table 11). Following this, a multiple comparison in multidimensional space was carried out to look at pair-wise relationships. The test statistic, Hotelling's T-square suggested that in winter, nilgai and chinkara were quite similar to each other (Probability > 0.05). All the other species pairs were quite dissimilar to each other (Probability < 0.05). In summer, chital and sambar had considerable similarity (Probability > 0.05). Nilgai and chinkara were also similar to each other (Probability > 0.05). The other species pairs were sufficiently dissimilar (Probability < 0.05) (Table 12).

Stepwise Discriminant Function Analysis (DFA) using Mahalanobis distance as the criteria, identified three variables that could distinguish between the four species during winter season: grass cover, slope and distance to water. For summer season, barrenness of ground, litter cover on ground and slope were found useful in separating the four species (Table 13). In winter, the first Discriminant Function (DF) could explain 98.1% of the total variability. In summer, the first DF could explain 93.3% of the total variation (Table 14). The classification plot based on the DFs supported the results from pair-wise comparison by Hotelling's T-square statistic (Table 12). In winter chital was most frequently misclassified as sambar and nilgai. Sambar was usually misclassified as chital. The chinkara and nilgai pair also showed misclassifications. In summer, most number of misclassifications occurred in the chinkara and nilgai pair, (Table 15). The relative positions of four species in the newly constructed discriminant space are depicted in Fig. 9.

Species relationships were converted into a dissimilarity matrix using Mahalanobis Distance Measure (Table 16). A Cluster Analysis procedure on these dissimilarity matrices produced the dendrograms depicting dissimilarities between the four species (Fig. 7B and 8B). This analysis brought out the associations between the species in each season, which resulted in the recognition of two groups. Sambar and chital showed less dissimilarities in space, and so did nilgai and chinkara.

These two different types of matrices (i.e. one for spatial resources and another for food resources) were put through a Multidimensional Scaling procedure. Since the matrices used were derived distance measures, a non-metric approach was chosen (Spence, 1978). This produced a composite picture of the species relationships in terms of these two key resources (Fig. 10 A & B). The results for each season were not much different from each other. In winter, the two dimensions (X and Y-axes) were sufficiently weird and were near equal in relative importance and thus enjoyed individual identities. The X-axis represented spatial relationship and Y-axis represented dietary relationship. Two distinct dimensions were obtained in summer as well (Table 17). The positions of each of the four species in relation to each other suggested considerable separation on alternate dimensions. Chital and sambar, as well as nilgai and chinkara were closer to each other in space but were further apart in food axes.

Table 11. Results of Discriminant Analysis by Pillai's trace for equality of centroids of four study species in spatial resource use

	Statistic	F-value	df 1	df 2	Pr
Winter	0.6741	1.9982	57	393	0.00
Summer	0.7298	2.0302	57	360	0.00

Table 12. Results of pair-wise species comparison by Hotelling's T square for equality of means for resource use in space

Species pair	**Hotelling's T square (Probability)**	
	Winter	**Summer**
chital-sambar	0.04	0.06
chital-nilgai	0.01	0.01
chital-chinkara	0.00	0.00
sambar-nilgai	0.00	0.00
sambar-chinkara	0.00	0.00
nilgai-chinkara	0.93	0.53

Table 13. Canonical coefficients of Discriminant Functions extracted by DFA

Function	I	II	III
Grass cover	0.582	-0.179	0.804
Slope	0.79	0.470	-0.398
Distance to water	-0.365	0.884	0.314

A) Winter

Function	I	II	III
Barrenness	0.602	1.020	0.011
Litter cover	0.522	0.249	0.953
Slope	-0.644	0.813	0.264

B) Summer

Table 14. Eigen values of three Discriminant Functions extracted by stepwise DFA in two seasons

Function	Eigen value	% variance	Cumulative % variance	Canonical correlation
I	0.858	98.1	98.1	0.68
II	0.013	1.5	99.6	0.115
III	0.004	0.4	100	0.061

A) Winter

Function	Eigen value	% variance	Cumulative % variance	Canonical correlation
I	0.684	93.3	93.3	0.637
II	0.048	6.5	99.8	0.213
III	0.001	0.2	100	0.036

B) Summer

Table 15. Classification plot from Discriminant Analysis on four species using three Discriminant Functions

Species	Chital	Sambar	Nilgai	Chinkara
Chital	19	10	15	0
Sambar	12	25	3	0
Nilgai	9	2	33	0
Chinkara	1	0	21	0

A) Winter

Species	Chital	Sambar	Nilgai	Chinkara
Chital	21	13	12	0
Sambar	14	23	0	0
Nilgai	12	2	23	3
Chinkara	1	1	11	3

B) Summer

Table 16. Matrix of Mahalanobis distance measures between species based on dissimilarity in use of spatial resources

Species	Chital	Sambar	Nilgai	Chinkara
Chital	0	1.72	1.91	4.04
Sambar	-	0	5.84	8.47
Nilgai	-	-	0	0.81
Chinkara	-	-	-	0

A) Winter

Species	Chital	Sambar	Nilgai	Chinkara
Chital	0	1.70	1.97	4.88
Sambar	-	0	5.15	7.17
Nilgai	-	-	0	1.72
Chinkara	-	-	-	0

B) Summer

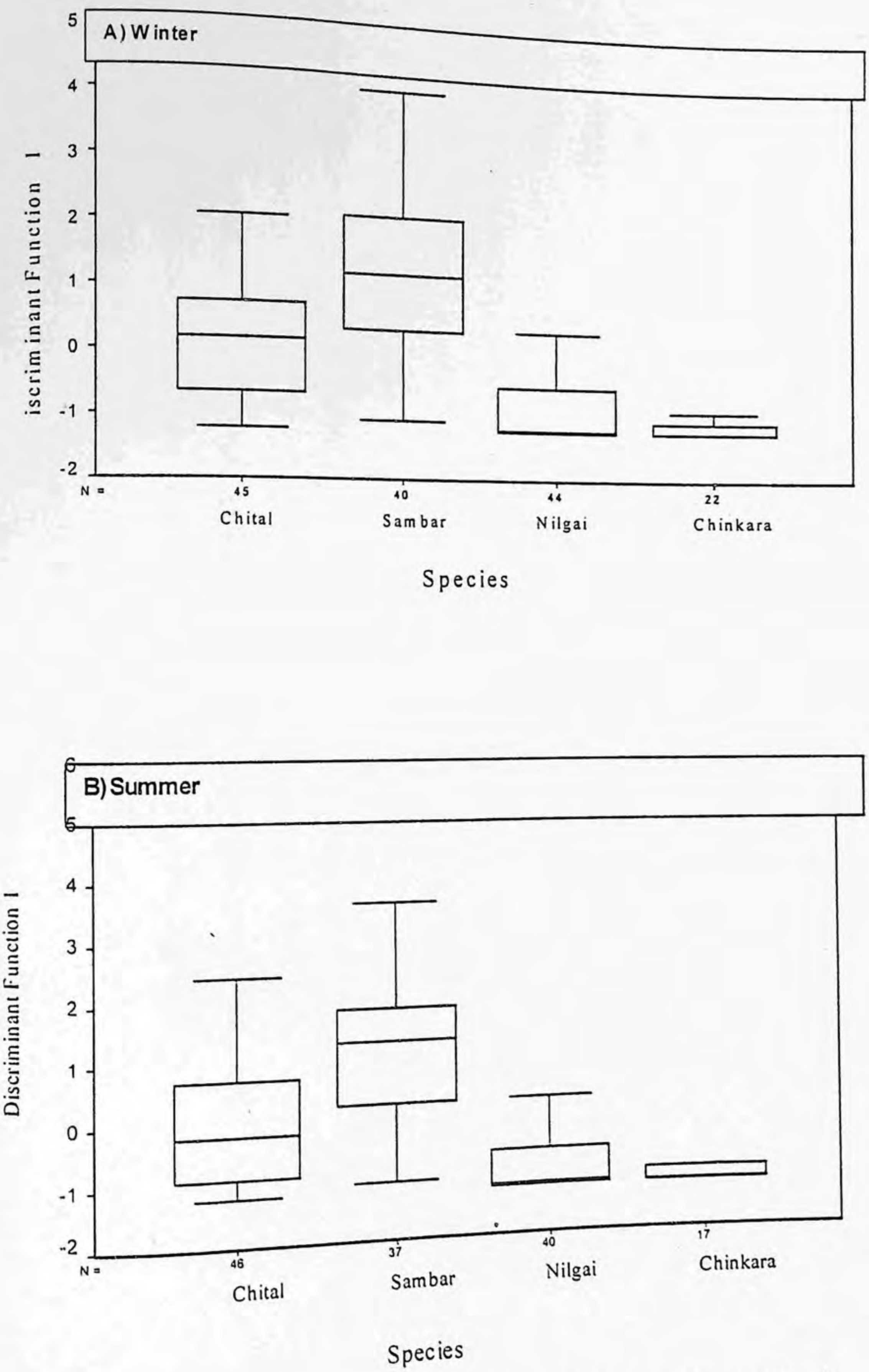


Fig. 9: Relative positions of four species in Discriminant Space across two seasons in Ranthambhore National Park

Table 17(A). Relative importance of two axes (X and Y) in Multi-dimensional scaling during winter.

Subject	Weirdness	X axis	Y axis
Space	0.97	0.01	0.99
Food	1.00	0.99	0.01
Overall importance		0.50	0.49

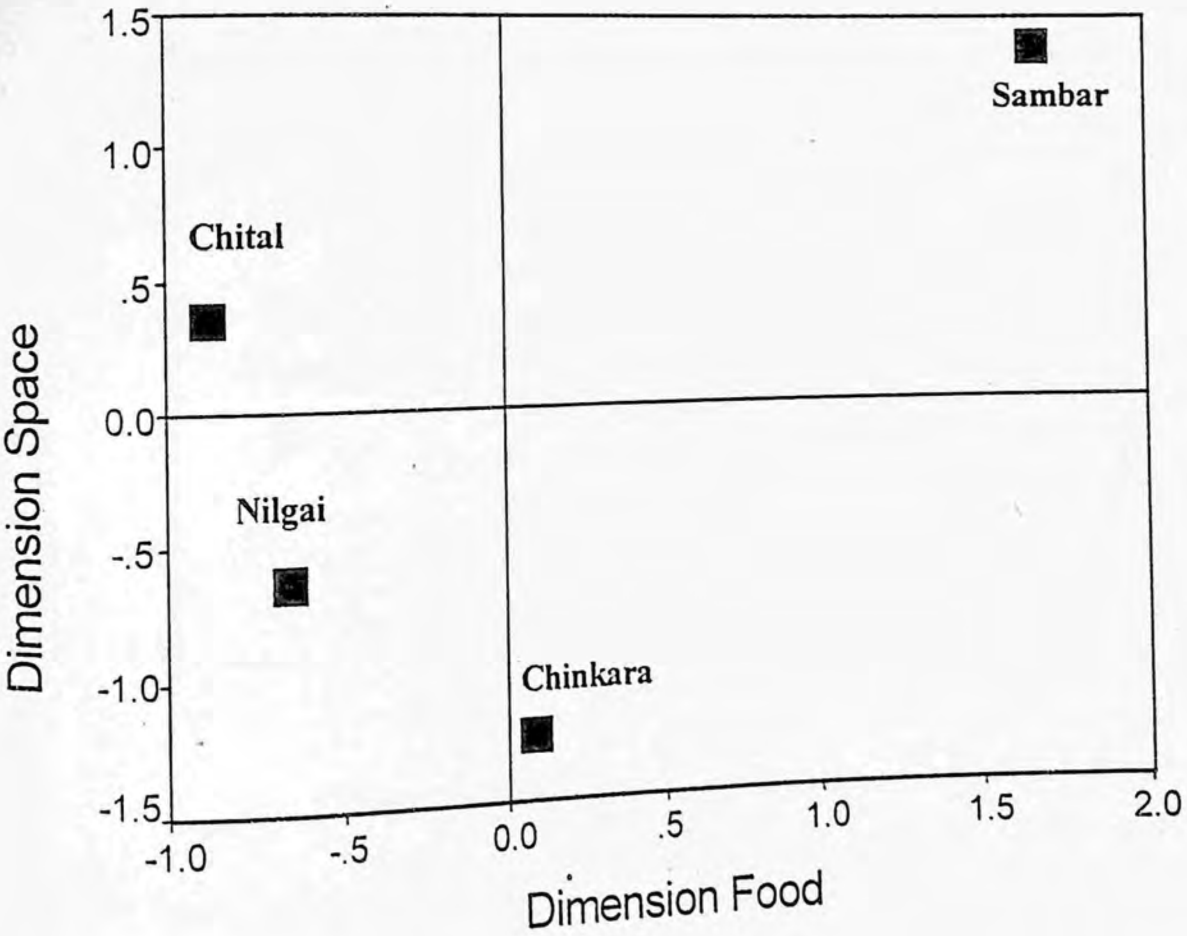


Fig. 10(A). Species relationships in communal niche-space during winter.

Table 17 (B). Relative importance of two axes (X and Y) in Multi-dimensional scaling during summer

Subject	Weirdness	X axis	Y axis
Space	0.85	0.99	0.09
Food	0.68	0.29	0.95
Overall importance		0.53	0.45

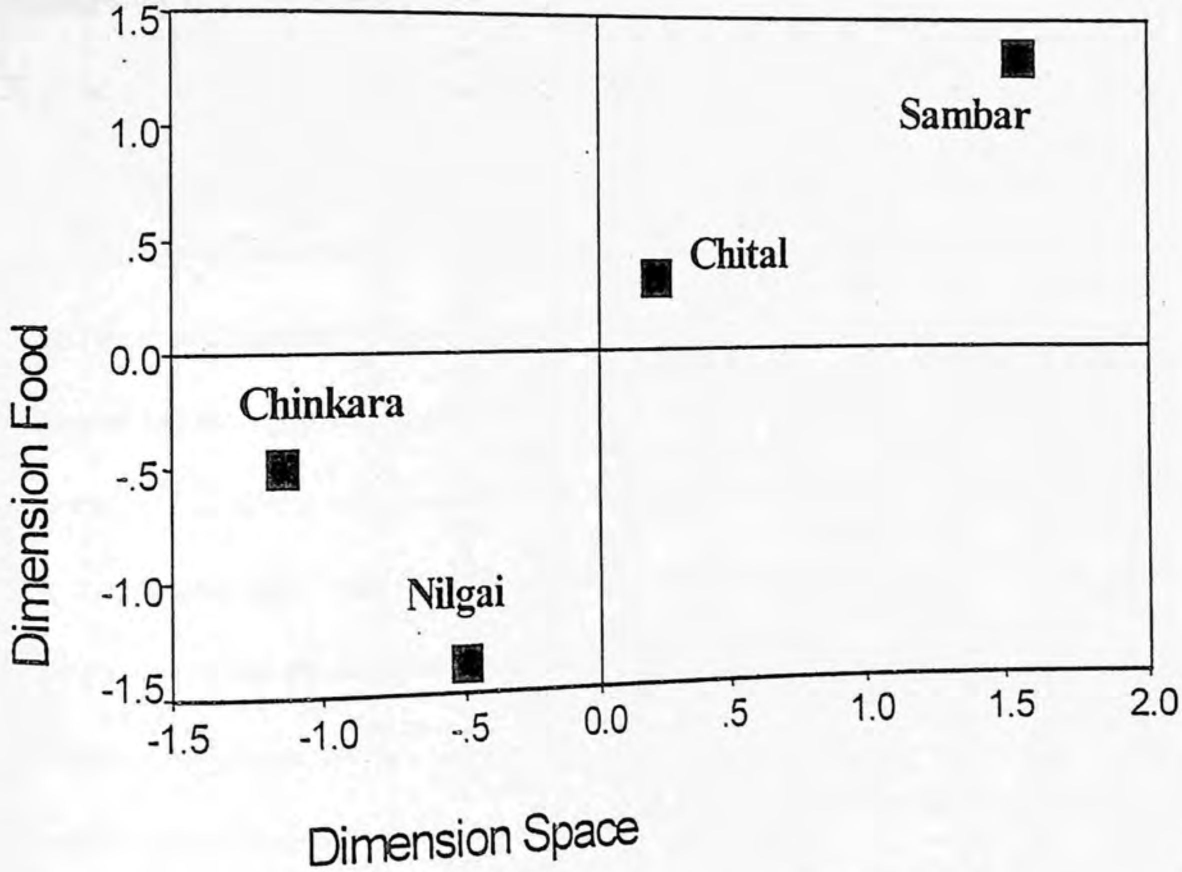


Fig. 10 (B). Species relationships in communal niche-space during summer.

6. Discussion

6.1. The spatial dimension of resources

Animals are expected to respond to the properties on offer in a particular patch (Rosenzweig, 1981). Thus it is important to recognize the different categories of patches or habitat types that an animal can choose from, in order to meet its requirements of food, cover and water. Instead of *a priori* determination of different habitat types, it is desirable to consider terrain and vegetation by classification. This increases the chances of evaluating the resources in the way an animal perceives it (Jarman and Sinclair, 1979). Ben-Shahar (1995) has emphasized the importance of classifying habitats correctly; and suggested the use of classification techniques for this purpose. Five distinct habitat types could be delimited from the eleven sites in the ISA (Fig 4). Thus within the dimension of space there were five sub-units. In the terminology of Slobodchikoff and Schulz (1980), space was a 'macrodimension' with five 'microdimensions' embedded in it. It is interesting to look at the differences between the microdimensions:

1. *Anogeissus* forest with *Grewia* in the undergrowth (Habitat A) was widespread in the slopes and the plains. It provided good cover to the animals, as there was high canopy cover and tall shrubs. In both seasons, forage was available mainly as fallen leaves of *Anogeissus* trees.
2. *Anogeissus* trees with *Capparis* and *Dichrostachys* shrubs (Habitat B) was a more open habitat in terms of canopy cover. But the green shrubs probably provided valuable forage to the animals. *Capparis* was especially important as it gives fresh sprouts at the beginning of summer. Rodgers (1990) has recognized the importance of *Capparis* as a dry season fodder for wild ungulates of arid and semi-arid region.

Sankar (1994) reported that *Capparis* offers 10 to 14% crude protein to the animals during the pinch periods and it is a preferred food plant of chital, sambar and nilgai.

3. *Anogeissus-Diospyros* forest with dwarf shrub layer (Habitat C) was restricted to a small pocket of the study area (Figure 2). It offered little horizontal cover, but plentiful food in form of fallen leaves.

4. *Acacia-Zizyphus* mixed woodland (Habitat D) was an open habitat, but it provided fruits and leaves in winter. In summer the forage importance of this habitat dropped after the fruiting in *Zizyphus* was over.

5. Grassy slopes and plateaus (Habitat E) were also very open. Although they supported high grass cover, the forage quality was low because of their dried nature as evident from their yellow-brown colour.

Thus it seems, that these five habitats had different values in meeting an animal's requirements. There was substantial variation between the five habitats in offering the basic requirements of an animal. So it will be worthwhile to investigate the decisions they took in terms of utilizing each of them.

6.2. Macro-level resource selection

Results suggested that each of the four species used the five habitats differentially in both the seasons (Table 4). In recent times, hypothesis testing of this type has been criticized because these are *a priori* known to be false, and their rejection does not provide any substantial information (Johnson, 1999). In fact, habitat use is rarely uniform in animals, but such a procedure was necessary for a discursive progression of logic in the present study. The mean ranks assigned in the Kruskall-Wallis test (Table 6) suggested that *Anogeissus* forest with dwarf shrub cover (Habitat C) was least used by chital. This might suggest a strong influence of cover in chital habitat use. Sambar was favouring grassy slopes and plateaus (Habitat E), while it was the least important for nilgai. Sankar (1994) and Sharma and Johnsingh (1996) have also pointed out the influence of slope in sambar habitat selection. *Anogeissus-Grewia* (Habitat A), was the least used among the five habitat types by chinkara. This suggests towards the importance of open areas without horizontal shrub cover for this species, which is known to inhabit open areas (Goyal *et al.*, 1986). These trends are consistent across the two seasons were primarily responsible for rejection of the hypothesis of uniform usage.

With these broad patterns we can say, shrub layer for cover is important for chital habitat selection, while slopes are important for sambar. Nilgai does not select for undulating terrain and chinkara does not opt for thick vegetation. Thus, these results should lead towards a more in-depth examination of resource selection.

6.3. Micro-scale resource selection

PC 2 (areas with *Capparis* and other green shrubs), PC 5 (*Anogeissus* forest close to water) and incidents of livestock grazing best predicted chital habitat selection in winter (Table 8). This suggested that chital responded positively to cover of shrubs (mainly from *Grewia*) and good quality forage (from *Capparis).* They were negatively affected by presence of cattle, especially because their owners often accompanied them into the forest. Sankar (1994), Khan (1996) and Mathai (1999) had also concluded that chital was sensitive to anthropogenic disturbances of this type. In summer, PC 2 (scrubland) and PC 5 (*Anogeissus-Grewia* forest close to water) predicted chital habitat selection (Table 8). While the influence of shrub cover was retained, the importance of water became profound in summer, when chital became more dependent on water. Chakrabarty (1991) had reported that the ranging patterns of animals are deeply influenced by water during the hot season. In fact, he found that the home ranges of the animals became smaller during the hot season. Sankar (1994) and Sharma and Johnsingh (1996) had also found relations between ranging pattern and water during summer.

PC 2 (areas with *Capparis* and other green shrubs), and PC 5 (*Anogeissus* forest close to water) were able to predict sambar habitat selection in winter (Table 8). This suggests sambar, like chital was also influenced by shrub cover (from *Grewia*) as reported by Khan (1996) from Gir. But the influence of water was stronger than in chital. In fact, the behavioural requirements of sambar, like wallowing, may explain its greater dependence on water than chital. Schaller (1967) has emphasized this aspect of sambar's ecological requirement as a *sine qua non*. Another reason behind water dependency of sambar could be its habit of foraging on aquatic vegetation in the perennial water-bodies. Interestingly, this type of foraging behaviour is reported only from certain semi-arid areas (Ranthambhore and Keoladeo National Parks). PC 3 (*Acacia-Zizyphus* woodland) and PC 5 (*Anogeissus-Grewia* forest close to water) explained sambar habitat selection in summer (Table 8). This meant that during the hot season, sambar was seeking to exploit green trees. *Acacia leucophloea* was the chief tree to sprout in summer. whose fresh leaves were being sought after. In this way the nutrition-based requirements of an animal can be visualized.

PC 1 (*Anogeissus-Diospyros* forest with dwarf shrubs) and presence of livestock construed habitat selection by nilgai in winter (Table 8). They probably took shelter in well-wooded areas to exploit the fallen leaf litter as forage. But more open and degraded areas were also occupied. Nilgai was not affected adversely by presence of livestock and related disturbances. Sankar (1994) had also found an association between nilgai and degraded areas. But on a contrary note. Sharma and Johnsingh

(1996) had found a negative influence of disturbance on nilgai habitat selection in Gir. But during the present study, they might have occurred in such areas because of a probable reliance on crops to fulfill their nutritional requirements. PC 1 (*Anogeissus-Diospyros* forest with dwarf shrubs) and PC 3 (*Acacia-Zizyphus-Butea* woodland) along with presence of livestock were able to describe habitat use for nilgai in summer (Table 8). The importance of *Acacia leucophloea* and *Capparis sepiaria* that sprout during summer in the scrubland and woodland surfaced in summer.

PC 1 (*Anogeissus-Diospyros* forest with dwarf shrubs) and PC 2 (*Capparis* and other green shrubs) could explain habitat selection by chinkara in winter (Table8). Heavily wooded areas might have been used for shelter and also for foraging on leaf litter. Even though Sankar (1994) has emphasized the importance of fallen *Anogeissus* leaves that have 6 to 9% crude protein; the dependence on cover is not in accordance with earlier findings. Sharma and Johnsingh (1996) had found chinkara to be independent of cover, but in the present study, they seem to be using well-wooded areas as well. More open areas were also used by chinkara, to forage on green shrubs, especially *Capparis sepiaria, Balanites aegyptica* and *Barleria cristata*. Shrubs are not only important as food but also for certain behavioural aspects like scent marking and territoriality (Jakher and Dookia, 2000). PC 2 and PC 4 explained chinkara habitat selection in summer. In this manner, the importance of green shrubs became even clearer. This also suggested that chinkara was not using undulating and hilly terrain and restricted itself to flat and open country. .

One pattern that has clearly emerged, is that the bovids (nilgai and chinkara) are much less influenced by water than any of the cervids (chital and sambar). This is expected as the oriental cervids (chital and sambar) have not evolved in an arid environment. But the bovids (chinkara and nilgai) have evolved under such conditions

(Rodgers, 1988) and are better adapted to dry and arid conditions. Chakrabarty (1991) had found this relationship in Sariska for nilgai. Sharma and Johnsingh (1996) had come across similar tends for chinkara in Gir.

The model seems to satisfactorily provide relevant information about habitat selection by the animals. Even though the rate of correct classification is high in case of used plots, the overall PE ϕ was not high (Table 8). This can be attributed to misclassifications in unused plots. Given the time-scale of the study, it is not expected that the animals should explore each and every site and respond to its properties. In fact, certain potential sites may never be used even in larger time scales (Lane *et al.*, 2001). Thus, several potential plots were not visited by the animals in the given time span and thus resulted in misclassifications. This necessitated the step towards validation of the proposed model. On validation, the model gave satisfactory results for all the species in both seasons. Thus, the applicability of such predictive models in ungulate assemblies of semi-arid region was demonstrated. Similar models have been widely used in managed forests of North America (Morrison *et al.*, 1998) and have a scope of wider applications in India.

6.4. Food as a resource dimension

Grass: browse ratio is a crude estimate of the dietary resource dimension. It helps in positioning the species along the *grazer-browser continuum*. Diet composition in all species experienced a shift across the seasons. In general, the contribution of grass on the diet dropped for all species across the seasons (Fig. 5). This could be because of the fact that dried grass did not provide enough nutrients in summer, but was probably more nutritious during winter. Moreover, it is quite possible that the grass (monocot fragments) found in chinkara and nilgai diets during winter came from the crops of agricultural fields close to the ISA. They were known for raiding the crop fields and did so frequently in winters (pers. observ.). But during summer, after the harvest, they shifted to a diet less constituted by crops. It is interesting to find high grass in sambar diet during winter; this could be because of foraging on aquatic monocots. Also, its affinity towards sloping terrain that supported grass cover might be one reason for high grass: browse ratio in sambar diet during winter. In summer however, sambar shifted to a browse dominated diet (Fig. 6). Johnsingh and Sankar (1991), Khan (1994) and Sankar (1994) had found similar shifts towards more browse in sambar's diet during summer. This seasonal shift in diet composition of all the species brings out the importance of fallen leaf litter for the animals. Once the dried grass became nutritionally poor, the leaf litter could support the animals. Fresh sprouts from *Capparis* and *Acacia* supplemented this during summer.

6.5. Partitioning of resources

Although there can be innumerable dimensions in defining an organism's niche, the most relevant ones are those that help in differentiating it from other species (Green, 1971; Dunbar, 1978). In the present study differences were sought over two dimensions- space and food.

Use of Discriminant Analysis has been done to address niche relationships in several taxa (Green, 1971; Reinert, 1984; Edge *et al.*, 1987; Marnell, 1998; Wei *et al.*, 2000). Considerable debate has taken place on the assumptions of such techniques being not fulfilled by ecological data (Carnes and Slade, 1982; Williams, 1983; Rexstad *et al.*, 1988, 1990; Taylor, 1990). The assumption of equal dispersion of matrices was not met by the data for each season (Box's M, Pr <0.05 for winter, but

Pr> 0.05 for summer). Thus the canonical functions obtained must be considered exploratory (Williams, 1983; Edge *et al.*, 1987).

Based on Pillai's trace statistic (Table 11), the four species-centroids over spatial resources were found to be non-identical, in each season. Stepwise DFA identified three variables (slope, grass cover and distance to water), that were successful to discriminate between the four species during winter. In summer, barrenness of ground, litter cover on ground and slope were found to be differentiating between the species. The four species were seen to show segregation in discriminant space (Fig 7). There was overlap between sambar-chital and between nilgai-chinkara in the position in discriminant space in both seasons. This overlap became apparent in the classification plots using the DF scores (Table 15). Chital and sambar sites were seldom misclassified as those of chinkara; nor were sambar and nilgai sites confused with one another to any great extent. But there was confusion between sites of sambar and chital, nilgai and chital, along with nilgai and chinkara. When the distances between species centroids (Table 16) were used to evaluate dissimilarities, two clear 'guilds' emerged. The cervids and the bovids were found quite separated out in space. But chital-sambar (i.e. cervid group) and nilgai-chinkara (i.e. bovid group) were similar to each other. These guilds were similar in both seasons (Fig. 6). In general, we have seen earlier that chital and sambar had shown close association with well-wooded areas with high shrub cover. Nilgai and chinkara had been associated with more open areas like woodland and scrubland. This distinction between the 'forest' and 'scrub' animals became very evident from these dendrograms. Moreover, the distinction between these two groups on the basis of water dependence has already become clear. Thus we can see that the spatial dimension of the communal niche was broken into two parts, one occupied by the cervids and the other by the bovids;

suggesting strongly towards the evolutionary consanguinity between the study species.

When the dissimilarities in diet were plotted as dendrograms, (Fig. 7), the overlap between chital and nilgai became visible. Sambar and chinkara occupied unique positions in each season, while nilgai-chital were not dissimilar in food habits. Interestingly, nilgai and chital are expected to be generalist in their diet-choice and thus might have overlapped with one other in food habits. Rodgers (1988) and Sankar (1994) have suggested such generalized diet choice by chital and nilgai. In this way the dietary dimension of the communal niche space seems to be broken into three parts, one occupied by sambar, another by chinkara and the third is being shared by the generalist nilgai and chital.

The dendrograms for space and food hinted towards complementary overlaps in the two resource dimensions. The multidimensional scaling exercise elaborated this further. Fig. 16 (A and B) condenses the information in Fig. 6 and 7. In winter, although the two cervids were close to each other in space, they were widely separated in diet. A similar scenario emerged for the bovids as well, nilgai and chinkara were close to each other in space but separated out in food (Fig. 16A). In summer, the situation was very similar, except that the two cervids had approached each other more closely (Fig. 16B). As the season progressed, resource-limitation might have caused the species to converge on one another. The cervids, attached to well-wooded areas, greatly depended on litter for food. This possibly caused chital and sambar to encroach on one another. The bovids were associated with scrub-woodland, resulting in a dependency over fresh sprouts for food. Consequently, nilgai and chinkara transgressed one another. Despite this convergence, their positions in communal space were still distinct and discernable. This perfect complementation in alternate resource dimension shown by the four species is the means by which they partition the available resources. Schoener (1974) and Toft (1985) have theorized such complementation in natural communities. Green (1987) found similar complementation in the Himalayan ungulate assemblage.

The ungulates in Ranthambhore National Park, Rajasthan, seem to follow the above principles in order to co-exist. Thus, by the present study the means of resource partitioning in the ungulate assembly of Ranthambhore National Park, Rajasthan, have been identified. There seems to be complementary overlap on the alternate resource axes between the four species. The overlaps are in line with the expectations in terms of their phylogeny, the cervids and bovids are separated out in one major axis i.e. space. The overlap for space is not detrimental because by differentiation in terms of diet, the four species can coexist and also perhaps avoid competitive interactions.

6.6. Niche-abundance relationships

How environmental conditions and population processes determine the abundance and distribution of species is a central problem of ecology and biogeography (Brown, 1984). The present study can edify this aspect in a restricted spatial scale, that of the local level, i.e. the habitat patches in the study area. Carrying on the lines of Brown (1984), Gaston *et al.* (1997) suggested possible association between niche position, niche breadth and abundance. They identified two possibilities- the most abundant species could be the most generalized one in the community (broad niche width), or, it could be specializing to exploit a specific but abundant resource (narrow niche width). Although niche positions and niche breadths need special calculations (Dueser and Shugart, 1979; Carnes and Slade, 1982; Van Horne and Forde, 1982; Seagle and McCracken, 1986), the scaled axes in Fig. 16 can be used as appropriate surrogates.

A close examination of the figures will reveal that chital has a tendency of occupying positions closer to origin (i.e. co-ordinates 0,0 in the newly constructed space). We can interpret the origin to represent the 'mean' resource-state. Thus chital seems to use the most general resources. By the density estimates, chital was found to be the most abundant of the four species (Table 2), in accordance with the findings of Kumar (2000). Hence the relationship between the most abundant species and the most generalized resources becomes evident. Thus it can be hypothesized that the ungulate assemblage of a semi-arid and dry-deciduous environment, the most generalized species would attain highest abundance. This generalization can be applied to animal assemblies in other environments, once the validity of using multi-dimensional scaling of niche relationships in lieu of actual calculations for niche position and niche breadth is established. This opens a possibility of further investigation into these theoretical aspects of animal-habitat relationships.

7. Summary

This study was aimed towards understanding resource utilization and partitioning in terms of space and food by four ungulates, *viz.* chital (*Axis axis*), sambar (*Cervus unicolor*), nilgai (*Boselaphus tragocamelus*) and chinkara (*Gazella benetti*). It was carried during November 2000 and April 2001; in the dry deciduous, semi-arid forests of Ranthambhore National Park, Rajasthan; covering winter and summer seasons.

Data were collected on direct evidence of habitat use and for density estimation (by transect walks) and also on indirect evidences of habitat use (pellet/dung deposition). Several vegetation and associated variables were measured at 99 sampling locations along 8 line transects in an Intensive Study Area of approximately 34 sq. km. Food habits were studied by microhistological techniques using pellets.

Chital was found to be the most abundant species in the study area; followed by sambar, nilgai and chinkara. Classification by cluster analysis on habitat variables led to the recognition of five habitat types. These five habitat types seemed to have different values in terms of resources on offer for the study animals. The four study species (chital, sambar, nilgai and chinkara) showed differences in relative use of the five habitat types in each season. A predictive model by logistic regression analysis was developed to explain habitat selection in terms of different features of the habitat like tree density, shrub density, greenness of trees, greenness of shrubs, distance to water, disturbance in the form of livestock grazing and others (i.e. micro-scale). The model was found to be reasonably accurate in its purpose. Noticeably, the key features and/or their combinations were often found unique for a species. This provided the first hint towards partitioning of resources.

By Discriminant Analysis the differences between the resource selection patterns of the four species were addressed. Few habitat variables (three in each season) were

able to discriminate between the four species in Discriminant space. As the assumptions of such analysis were not met by the data, further dealings were considered exploratory and not conclusive.

The two cervids were found to be close to each other in use of space, while the two bovids formed another similar but distinct group. In diet, sambar occupied a distinct position. Chinkara's food-niche was also found to be distanced from that of others. Nilgai and chital were found to be overlapping in food habits. But these two species were separated out in space. Thus by such complementation, the four species could divide the communal space among themselves, and achieve a state of co-existence. Using multidimensional scaling, the niche positions of each species were approximated. Chital was seen to be closest to occupying the most general features in the communal niche space. This could be a possible explanation for it to be the more abundant than the others as found by the density estimates using line transect data. This form of niche analysis was done in lieu of niche-position and niche-breadth calculations, but ecologically meaningful patterns were seen to emerge.

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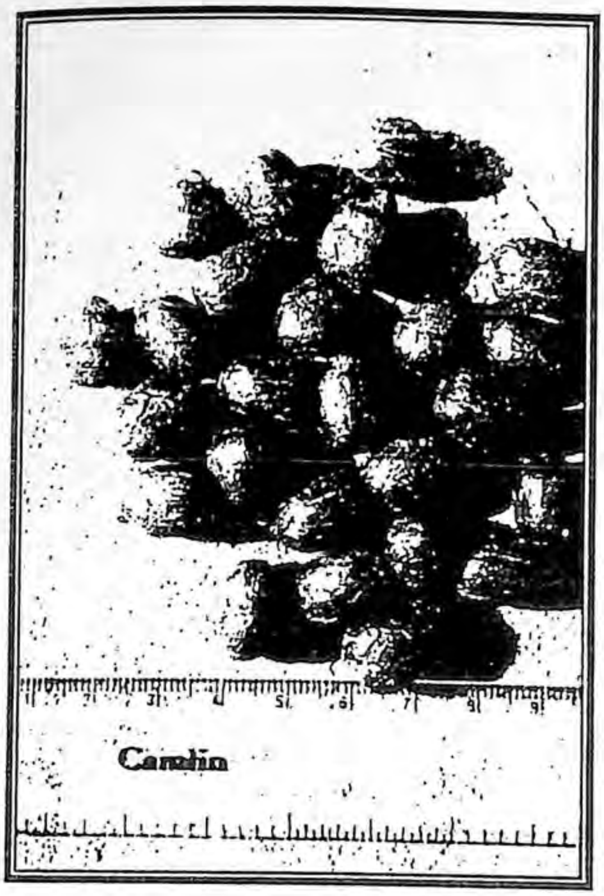
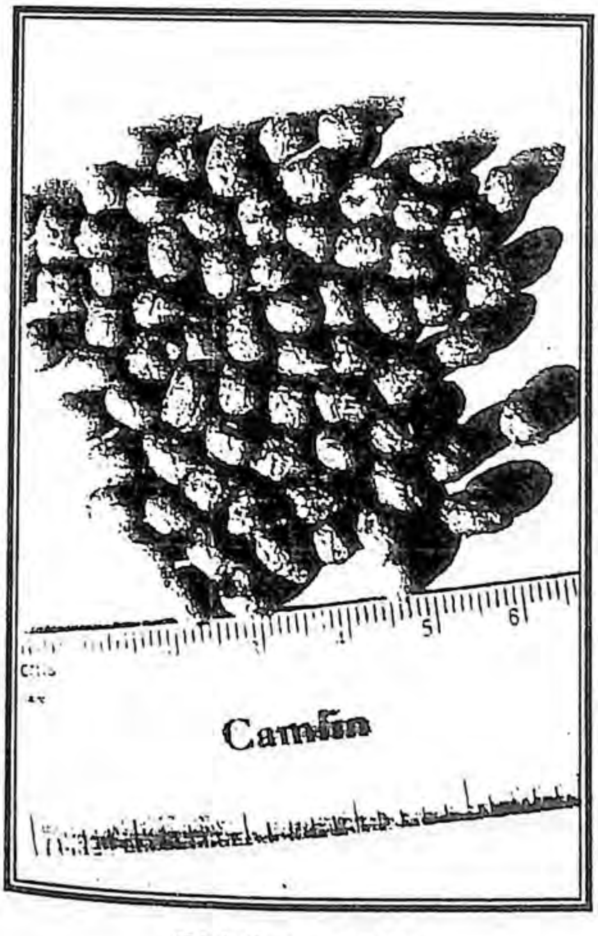
Appendix - I

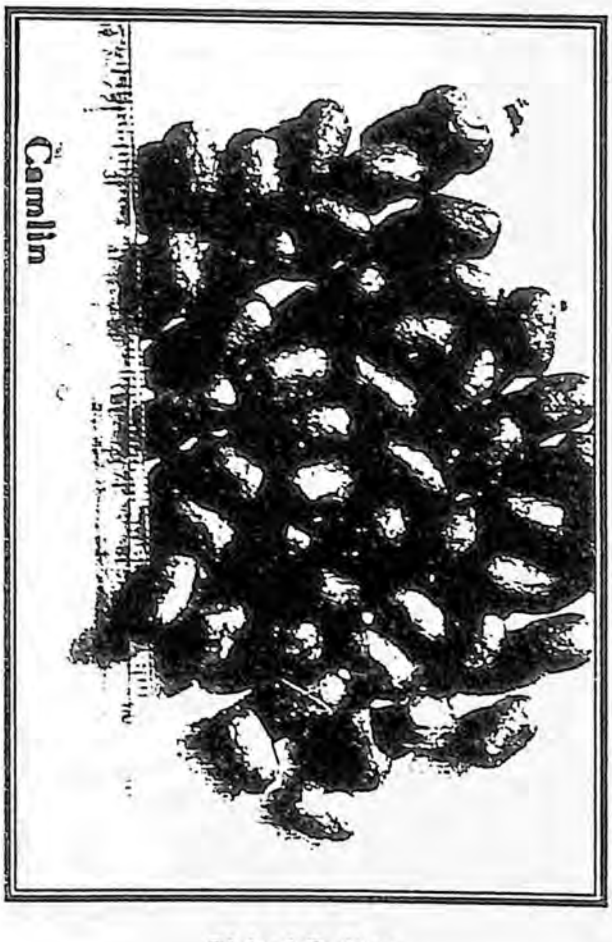


Sambar Pellets

Nilgai Pellets



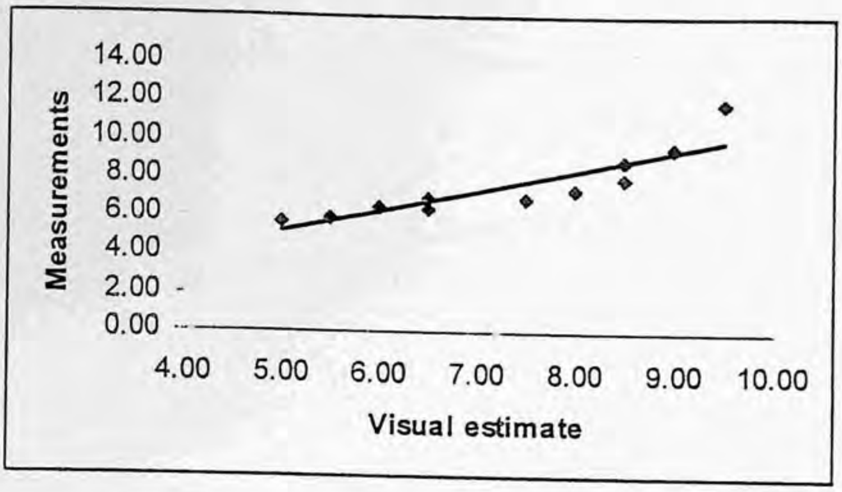
Chinkara Pellets



Chital Pellets

Appendix II

Relation between visual estimates and trigonometric measurement of tree heights



Test for normality of two types of tree heights measurements (visual estimates and trigonometric measurements) by Kolmogorov-Smirnov test

Parameter	Visual estimates	Measurements
Sample size	20	20
Mean	7.31	7.63
Std. Dev.	1.50	1.88
Kolmogorov-Smirnov Z (Normality)	0.53	0.64
2-tailed sig.	0.93	0.82

Validation two types of measurements of tree height (visual estimates and trigonometric measurements) by linear regression method

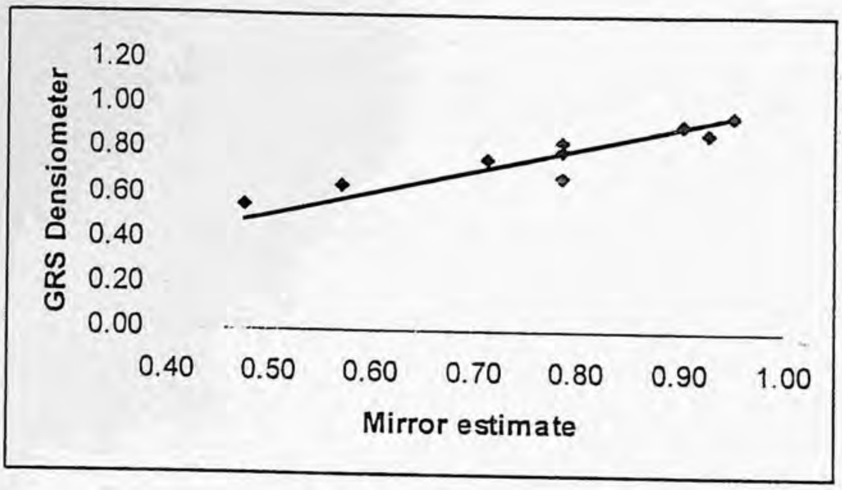
	R-square (Sig.)	**Coefficient (Sig.)**
Model	0.98 (0.00)	1.04 (0.00)

Model . Regression equation through the origin,

Regression equation: Trigonometric measurement = coefficient*(visual estimate)

Appendix III

Relation between estimates from grid mirror and GRS Densiometer for canopy cover



Test for normality of two types of canopy cover measurements (grid mirror and GRS Densiometer) by Kolmogorov-Smirnov test

Parameter	Mirror	GRS Densiometer
Sample size	19	19
Mean	0.7678	0.7822
Std. Dev.	0.1596	0.1343
Kolmogorov-Smirnov Z (Normality)	0.666	0.333
2-tailed sig.	0.767	1.000

Validation two types of measurements of canopy cover (grid mirror and GRRS Densiometer) by linear regression method

	R-square (Sig.)	**Coefficient (Sig.)**
Model	0.994 (0.00)	1.01 (0.00)

Model . Regression equation through the origin,
Regression equation: GRS Densiometer = coefficient*(grid mirror)