SEXUAL SEGREGATION IN THE NILGIRI TAHR (*HEMITRAGUS HYLOCRIUS*).

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CERTIFICATE

This is to certify that M. D. Madhusudan of the Wildlife Institute of India has carried out a piece of original research work entitled "Sexual segregation in the Nilgiri tahr (*Hemitragus hylocrius*)" in partial fulfilment of M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot. These investigations were carried out under my supervision at the Wildlife Institute of India from November 1994 to July 1995. I also certify that this work has not been submitted for any other degree of any other university.

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SUMMARY

I studied sexual segregation in the Nilgiri tahr *Hemitragus hylocrius* from November 1994 through April 1995 at Eravikulam National Park, Kerala, India. This study covered the post-rut phase of the tahr's annual cycle. The objectives of the study were to examine whether sexual segregation exists in the tahr, identify modes of segregation, and compare empirical findings with some theoretical hypotheses advanced to explain sexual segregation.

I investigated differences in the way the sexes occurred in social units, used space, chose forage and budgeted time. Data on group composition and habitat selection were collected on two trails monitored regularly. Availability of forage was quantified in three habitat strata. Differences in dietary quality were estimated with two faecal indices - crude protein and ash. Data on activity budgets were collected from group scans.

- Throughout the study period, tahr occurred mostly in female groups, bachelor groups, and to a lesser degree, in mixed groups. They showed marked segregation in the use of habitat types. Male groups used the rolling grasslands at the higher elevations intensively, whereas the female groups were distributed in rocky areas dominated by *Plebophyllum kunthianum*, and in areas of grass interspersed with cliffs. Male and female groups showed distinct differences in their choice of habitat. Males chose areas of high absolute amounts of graminoid forage, whereas females preferred areas of greater security; these were typically areas high slope angles and percent rockiness.
- There were no differences in the levels of crude protein and ash in the pellets of male and female tahr.
- Differences were also found in the time-activity budgets of the sexes. Although all age-sex classes spent equal proportions of time feeding, large males spent a greater proportion of their time resting than either small males or females. Females on the other hand, spent a greater proportion of their time moving than did individuals in the two male classes.

Sexual segregation in the Nilgiri tahr appears to result from a female choice for areas of greater offspring security, and a male choice for areas that allow maximisation of body-condition. Empirical findings do not support hypotheses which predict that segregation results from a male choice for areas of greater security from predation. Findings also contradict predictions invoking sexual size-dimorphism in the tahr as an explanation for the existence of segregation.

1. INTRODUCTION

1.1 *Sexual segregation*

Charles Darwin, more than a century ago, is credited with having observed that the males and females of a species often behave like *different species*. Since then, numerous studies have documented differences between the sexes, and offered explanations as to its possible adaptive role, and its significance in the ecology of the animal. Known as **sexual segregation**, this phenomenon collectively refers to the ways in which males and females of a species differentially use the available resources. Sexual segregation is seen among taxa ranging from dioecous plants (Freeman *et al.* 1976) and reptiles (Keenlyne 1972, Shine 1986) to birds (Wasserman 1986, Morton 1990, Summers *et al.* 1990), carnivores (Weilgus and Bunnell 1994), and ungulates (see references below).

In many species of ungulates, males and females segregate spatially after the rut (Peek and Lovaas 1968, Geist 1971, Geist and Petocz 1977, Cameron and Whitten 1979, Clutton-Brock *et al.* 1982, 1987, McCullough *et al.* 1989, Weckerly 1993). These studies have shown that segregation between the sexes also occurs in the choice of forage, differing patterns of activity and social behaviour. Though most frequently encountered in the ungulates of the temperate latitudes, reports exist of sexual segregation occurring in some tropical ungulates (Jarman 1974, Prins 1989)

1.2 *The Nilgiri tahr*

The Nilgiri tahr *Hemitragus hylocrius* Ogilby, 1838 is a highly endangered caprid listed in Schedule I of the Indian Wildlife (Protection) Act 1972, and categorised as 'vulnerable' by the IUCN (Groombridge 1993). It is endemic to the hill-ranges of the Western Ghats of southern peninsular India, in pockets where a suitable mosaic of montane grasslands and broken terrain exists. Unscrupulous hunting, and loss of habitat to plantations of tea, eucalyptus *Eucalyptus* spp., wattle *Acacia mearnsii* and pine *Pinus* spp. over large areas of its historic range have reduced both the distributional range and size of most tahr populations (Schaller 1970, Davidar 1978). The species today is distributed patchily in the two southern states of Tamil Nadu and Kerala. The last available estimates of the total tahr population range around 2200 (Davidar 1978, Rice 1984).

There have been very few studies on the Nilgiri tahr. Most of the attention the tahr has received from the scientific community has been of the nature of surveys (Schaller 1970, Davidar 1978, Rai and Johnsingh 1993, Mishra and Johnsingh 1994). The work of Rice (1984, 1988a, 1988b, 1988c) provides the only available information on the behaviour, and certain ecological aspects of the species.

In this study, I examine if sexual segregation exists in the Nilgiri tahr in terms of habitat-use, activity patterns and dietary quality, survey hypothesis that have been advanced to explain segregation. I also examine some hypotheses (see section 1.4) that offer proximate and ultimate explanations for sexual segregation in the tahr. Broad implications of the study for the management of tahr habitats are also discussed.

1.3 *Review of literature*

Although there exists a general agreement that sexual segregation occurs in many species of ungulates, there is little unanimity over its causation and adaptive value. Depending on the taxa in question and the geographic location of the study, various hypotheses have been proffered which attempt identifying the causes of sexual segregation. These can be classified under four broad headings, as hypotheses based on -

1.3.1 *Predation and sexual segregation.*

The hypotheses suggest that segregation occurs because :

- a. females choose areas that maximize post-partum neonate security from predation, while males choose areas of high forage quality (Geist 1982, McCullough *et al.* 1989, Festa-Bianchet 1988, Main and Coblentz 1990, Berger 1991). Safety from neonate predation is important for females as they try to maximise reproductive success which is measured in terms of offspring survival (Clutton-Brock *et al.* 1982). Males, on the other hand, try to maximise body condition which furnishes them with advantages in intrasexual combat during the rut, and therefore, choose areas of high forage quality and quantity regardless of security from predation (Geist 1982).

- **b.** post-rut males are in poor body condition, yet conspicuous and easily distinguishable from females because of their yet unshed antlers (in cervids). Associating with female groups might, therefore, make them more vulnerable to selective predation than they would be if they stayed away from female groups (Geist and Bromley 1978).

- **c.** predators are more likely to cue in on the post-rut vulnerability of males (rather than rely on the presence of antlers to indicate vulnerability). Hence, as a theory that explains sexual segregation across various ungulate families (and not just in cervids. *Cf* preceding hypothesis), it submits that males segregate from female groups since their presence in female groups post-rut might expose their vulnerability (Morgantini and Hudson 1981).

1.3.2 *Post-rut decline in male body-condition and energetic considerations.*

- **a.** This hypothesis states that, since post-rut fat reserves in males are depleted, they are forced to choose areas with cover to minimise energy losses due to thermo-regulation, etc. (Watson and Staines 1978). This has been disputed by Clutton-Brock *et al.* (1987) who found increased use of unsheltered areas by males on windy days in winter.

1.3.3 *Direct benefits and costs of sociality.*

- **a.** From their studies on bighorn sheep, Morgantini and Hudson (1981) proposed that, even after the rut, males were likely to indulge in energy-expensive intrasexual aggressive interactions in the presence of females although they were no longer receptive. Therefore, in order to avoid these energy-draining interactions, males segregated from female groups. Similar explanations have been invoked to explain sexual segregation in the chamois *Rupicapra rupicapra* (Shank 1985) and the African buffalo *Syncerus caffer* (Prins 1989).

- **b.** McCullough *et al.* (1989) and Verme (1988) hypothesize that post-rut males in white-tailed deer *Odocoileus virginianus* aggregate in open habitats in order to allow opportunities for social interactions. These interactions are postulated to aid in the establishment of dominance hierarchies, reduction of damage during antler growth, and finally, provide protection from predators. Though Main and Coblentz (1990) dismiss this hypothesis due to its narrow applicability, it is still considered one of the tenable explanations for sexual segregation in cervids (Miquelle *et al.* 1992).

1.3.4 *Sexual dimorphism.*

- a. Large-bodied males are thought to segregate from females (who out-compete them) since they are at a disadvantage in the scramble competition for limited forage due to their larger absolute energy requirements (Clutton-Brock *et al.* 1987, Illius and Gordon 1987). This has been conjectured from the studies that show the allometric relationship of bite size to body weight ($BW^{0.33}$) (Clutton-Brock and Harvey 1983) increases at a much slower rate than the relationship between the metabolic rate and body weight ($BW^{0.75}$) (Kleiber 1975).

- b. Segregation occurs independent of competition, owing mainly to

i. allometric relationships between body-size, metabolic rate, rumen size, bite size and energetic constraints (Hanley 1982, Clutton-Brock and Harvey 1983, Hudson 1985). This implies that due to a low metabolic rate to body weight relationship, males can subsist on poorer quality forage, while females may have greater protein requirements due to the costs of gestation and lactation. There exist studies that have demonstrated protein content to be greater in female diets than in male diets (Staines *et al.* 1982, Beier 1987) although absence of differences have also been recorded (Weckerly and Nelson 1990). Main and Coblentz (1990) suggest that these discrepancies might exist due to the fact that available energy might be a more important component of the diet than protein.

ii. variation between the sexes in seasonal energy-investment in reproduction (Geist 1982, Main and Coblentz 1990). Males come out of rut in a very depleted condition, in cases like the red deer *Cervus elaphus*, losing up to half of their body fat reserves (Mitchell *et al.* 1976). Males go into the winter with a greater energy debt than females. The males respond typically by acquiring more energy, reducing its expenditure or, by further depleting their fat reserves, all of which are reflected in their feeding, activity budgets, and habitat use different from females.

In addition to these, Geist and Petocz (1977) proposed that rams of the bighorn sheep segregated from ewes in order to reduce competition with mates and potential offspring, thereby increasing their inclusive fitness. Objections to this hypothesis have been strong; since breeding is not equally distributed among all males, it remains unexplained why non-breeding males should segregate after rut, to areas that are 'sub-optimal' (Morgantini and Hudson 1981, Main and Coblentz 1990). Clutton-Brock *et al.* (1987) submits that males might be less tolerant to faeces-contaminated areas having high parasitic load either because they are more susceptible to infestation or because females have to disregard these costs owing to the pressures of gestation and lactation. This is not quite tenable in the absence of information on sex-differences in parasite-susceptibility, and unless population densities of the species are extremely high (Miquelle *et al.* 1992).

Sexual segregation seems a feature common to the Caprini of the temperate latitudes (Geist 1971, Geist and Petocz 1977, Schaller 1977, Morgantini and Hudson 1981, Nievergelt 1981, Shank 1982, 1985, Francisci *et al.* 1985, Krausman *et al.* 1989). If patterns analogous to the ones reported in the above studies exist in the tahr, they are likely to be of importance in species-oriented conservation and management. In most situations, management practices usually tend to focus on areas of intense use by the bulk of the population. Knowing that breeding males occur singly or in small groups, and form a small proportion of tahr populations (Rice 1984, 1988b), they might receive very little positive inputs from the prevalent practices of management. Information on selection and use of habitats by the tahr is important, especially considering the fact that the already-restricted habitat for the tahr is still being lost (Mishra 1994). Additionally, Rajamala, the study area, supports a phenomenally high density of tahr: considering the endangered status of the tahr, managing habitats for tahr might essentially be captured in the metaphor of 'making other areas in the tahr range like Rajamala.'

1.4 *The Questions*

Although a test of all the above hypotheses would have been ideal, it was not possible. Some hypotheses had limited applicability, as for example, the hypothesis of Verme (1988), which does not explain sexual segregation in animals other than cervids. Moreover, there was a great deal of overlap in the predictions of these hypotheses. Therefore, to minimise overlap in these predictions, I consolidated three specific hypotheses for which a corroboration could be sought. Based on my data, I shall attempt to examine which of these are supported, which not.

1.4.1. *The Ecological Dimorphism Hypothesis*: Segregation occurs due to the dimorphism between the sexes as regards the ecological expediencies - females acting to reduce risk of neonate predation, and males, to maximise nutrient-intake, and hence, body condition. (Geist 1982, Festa-Bianchet 1988, McCullough *et al.* 1989, Main and Coblentz 1990, Berger 1991, Miquelle *et al.* 1992)

1.4.2. *The Male Vulnerability Hypothesis*: Low levels of food intake during the rut, and the energy-intensive nature of the rut results in males going into the period post-rut in a condition that might make them differentially vulnerable to predation. Hence they select components of a heterogenous environment that reduce the risk of predation (Geist and Bromley 1978, Morgantini and Hudson 1981).

1.4.3. *The Sexual Size Dimorphism Hypothesis*: As a consequence of body-size dimorphism, there are different nutritional requirements and energetic constraints operant among the age-sex classes. To meet these requirements, they use resources heterogeneously distributed in the environment (Staines *et al.* 1982, Hudson 1985, Clutton-Brock *et al.* 1987, Illius and Gordon 1987, Beier 1987, Weckerly and Nelson 1990).

2. STUDY AREA

2.1 *History and Administration*:

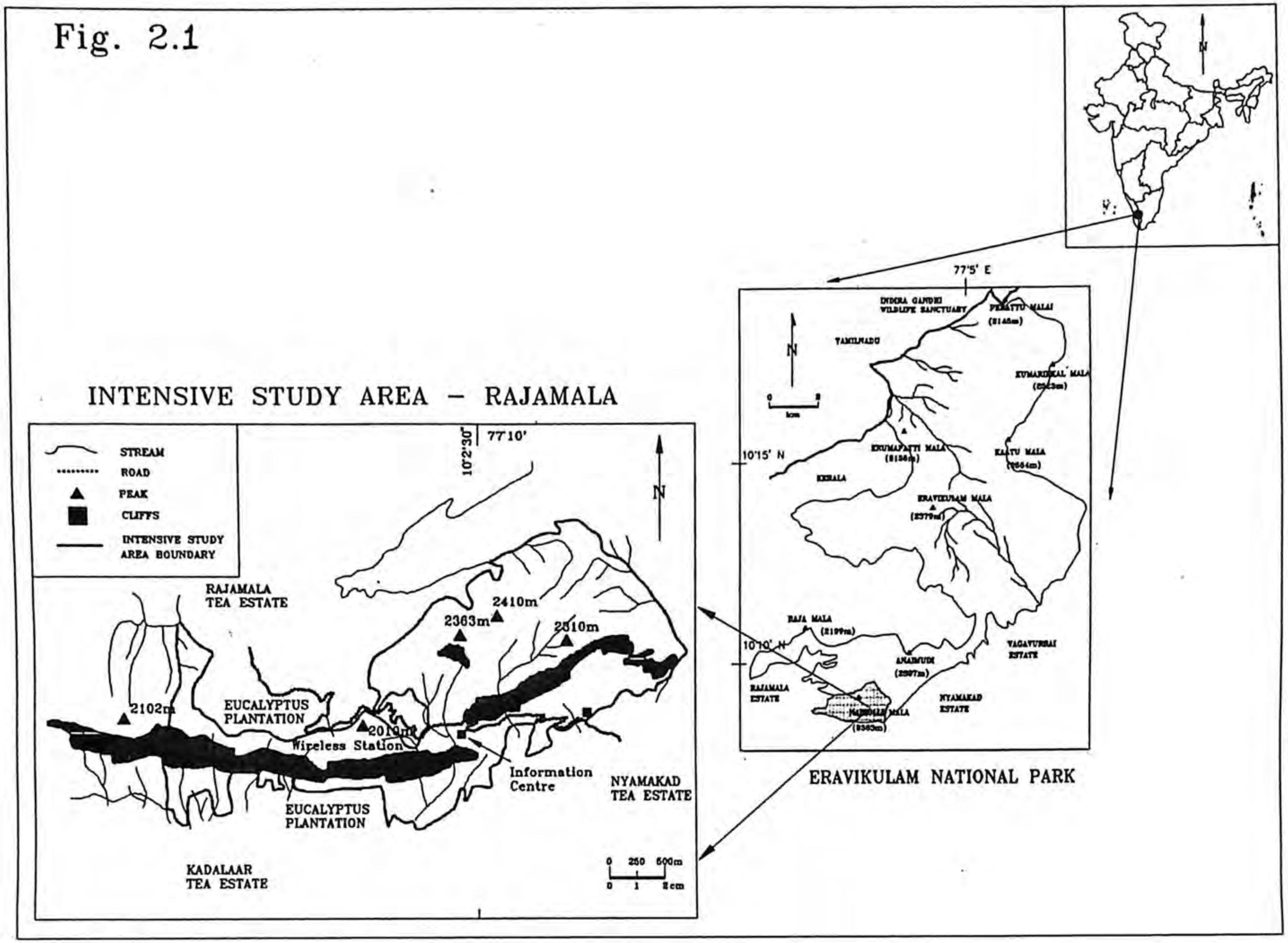
Eravikulam National Park (Fig. 2.1)is located between 10°10'N, 77°0'E and 10°20'N, 77°10'E on the crest of the Western Ghats south of the Palakkad gap. It is ninety-seven square kilometres in area and falls in Idukki district of central Kerala state.

Baig and Henderson (1978) recount that modern settlements in the High Ranges began around 1879 with the establishment of the Travancore Land Planting and Agricultural Society. In the years that followed, estates were developed that produced crops like cinchona, coffee, and tea. Gradually, tea established itself as the predominant crop in the area. From the turn of the century, this area was a part of the Kanan Devan Hills Produce Company's concession land, and managed as its game reserve. Here, hunting of large game such as the Nilgiri tahr, sambar *Cervus unicolor*, gaur *Bos gaurus*, muntjac *Muntiacus muntjak*, and wild pig *Sus scrofa*, and angling of the introduced brown trout *Salmo trutta* and the rainbow trout *Salmo gairdneir* was permitted. The High Range Game Preservation Association regulated these activities by ensuring low harvests, closed seasons, and appointing the managers of nearby estates as wardens for the game reserve. This was instrumental in keeping away poachers, and with them, the threat of indiscriminate hunting that endangered the tahr in other parts of its range. In 1971, the Government of Kerala took over the area, and later in 1975, declared it a wildlife sanctuary. Elevation to the status of a National Park came in 1978. Now, it is administered under the Idukki Wildlife Division of the Kerala Forest Department. The Park is flanked on the north by the Malayattoor Reserve Forest and the Grass Hills of Indira Gandhi Wildlife Sanctuary, Tamil Nadu, and on its east by the Chinnar Wildlife Sanctuary, Kerala.

2.2 *Study Period:*

The study was conducted between the third week of November 1994, and the third week of April 1995. This, in terms of the annual cycle of the tahr, corresponded to the post-rut, and the

Fig. 2.1


INTENSIVE STUDY AREA – RAJAMALA
STREAM
ROAD
PEAK
CLIFFS
INTENSIVE STUDY AREA BOUNDARY
10°2'30"
77°10'
N
RAJAMALA TEA ESTATE
2410m
2363m
2510m
2102m
EUCALYPTUS PLANTATION
2010m
Wireless Station
Information Centre
NYAMAKAD TEA ESTATE
EUCALYPTUS PLANTATION
KADALAAR TEA ESTATE
0 250 500m
0 1 2cm
ERAVIKULAM NATIONAL PARK
77°5' E
10°15' N
10°10' N
N

season of births. A minor rutting peak was also mentioned as occurring around January (Rice 1984). But, nothing suggestive of this was observed, and hence, the period was recorded as the post-rut (for the males), and birth season (for the females).

2.3 *Climate and Topography*:

Monsoon characterises the annual cycle in the area. Altitude and proximity to the coast, among other reasons, make it a high-rainfall area. On an average, the annual rainfall is between 5000-6000 mm. The bulk of the rain falls during the 'summer' monsoon (or the southwest monsoon), which occurs between May and August. The second spell of monsoon occurs from October through December, and is called the northeast monsoon. Though it rained during every month of the study, the months between December and April are predominantly dry. Temperatures on the Eravikulam Plateau range between 29°C and -3°C (Rice 1984). Winds were generally light in the winter months; but occasionally they were extremely fierce, especially on the hill-tops and ridge-crests. Frosts occurred occasionally between November and January. Temperature and rainfall data for ENP is summarised in Fig. 1.

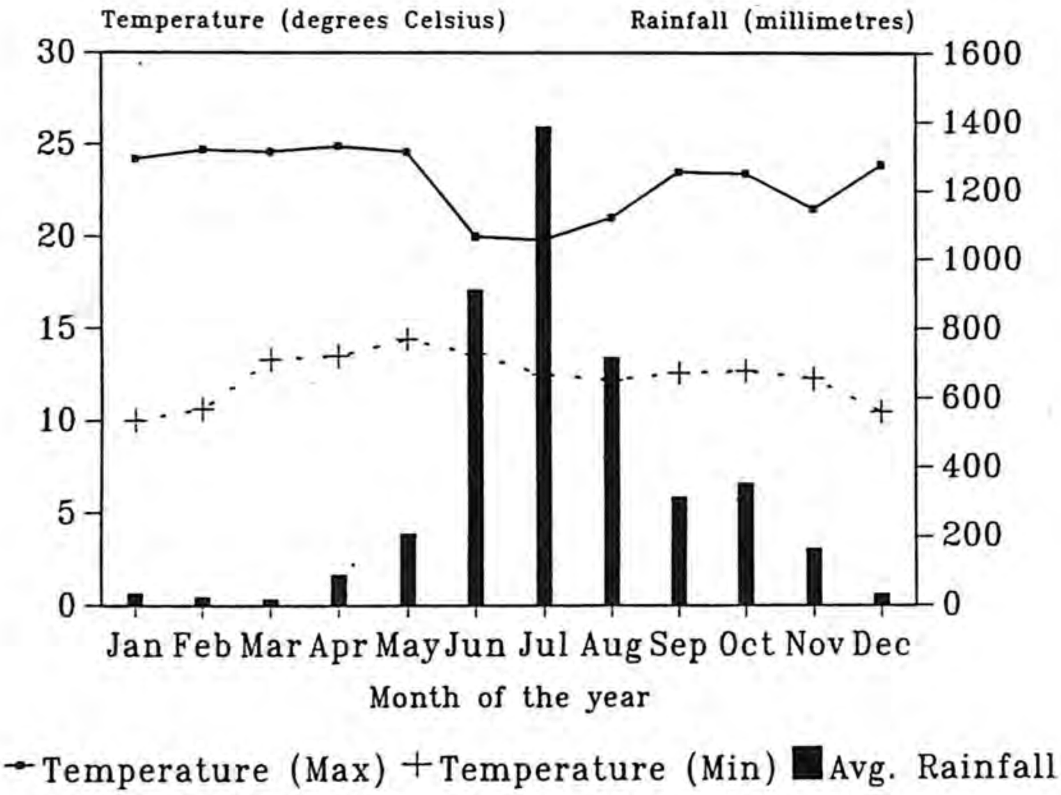
The general topography of the main portion of the National Park is of a high plateau (c. 2000m ASL) over which grassy knolls and granite cliffs rise and fall gently.

2.4 *Physical*:

2.4.1 *Vegetation*:

A mosaic of grassland, *shola*, and scrubland constitutes the dominant vegetation forms of ENP. Grasslands are found in the more exposed, wind-swept areas at elevations greater than c.2000m. The *sholas* are usually confined to sheltered valleys, hollows and depressions: areas of typically greater soil depth, adequate moisture and good drainage. These vegetation forms fall under the Southern Montane Wet Grassland (Sub Group IIA, type DS2), and Southern Montane Wet Temperate Forest (Sub Group IIA, type CI) of the classification proposed by Champion and Seth (1968). The third vegetation form, the scrubland, usually occurs in the rockier terrain, steeper

Fig. 1 Rainfall and Temperature at Eravikulam National Park, Kerala, India.



Data from June 1992 to April 1995.

Courtesy: P. V. Karunakaran

slopes and at the base of cliffs. A more comprehensive account of the vegetation of Eravikulam can be found in Shetty and Vivekananthan (1971).

2.4.2 *Fauna*:

Besides the Nilgiri tahr, other herbivores of ENP include sambar, gaur, muntjac, wild pig, and Asian elephant *Elephas maximus*. Large carnivores include tiger *Panthera tigris*, leopard *P. pardus*, and the dhole *Cuon alpinus*. ENP is home to several species of mammals endemic to the Western Ghats. These include Nilgiri langur *Presbytis johnii*, Nilgiri marten *Martes gwatkinsi*, brown mongoose *Herpestes fuscus*, and dusky striped squirrel *Funambulus sublineatus*.

2.5 *Intensive study area*:

Rajamala on the southern boundary of ENP was the intensive study area. Rajamala, which is also the operational headquarters of the National Park, supports a high density of tahr. At least three decades of protection from poaching has made tahr at Rajamala highly habituated to human presence. This makes Rajamala an ideal site for studies on tahr that necessitate close and continued observations.

3. METHODS

3.1 *Selection of intensive study-site:*

I marked out a boundary to the area around Rajamala based mostly on natural topographic features (like large sholas) and other prominent landmarks (like tea-estate boundaries) that the tahr heeded. Within these boundaries, a good representation of the different habitat types was ensured. Logistics were admittedly important since the terrain was very rugged and had to be covered on foot; but I made every effort not to let it become an overriding consideration, and make the final study-area-delineation biologically somewhat arbitrary.

3.2 *Classification of tahr:*

I categorised tahr into age-sex classes based on modifications to the detailed classifications given by Schaller (1970), Davidar (1978), and Rice (1984). Males were distinguished into two classes as large and small males based on their estimated age, pelage characteristics, relative body- and horn-size. The former class included dark brown males and saddlebacks, and the latter comprised solely of the light brown males, as classified by Rice (1984); all females older than c. 2 years were considered adult females. It was possible to separate younger animals into yearlings (between 1 and 2 years), and young (less than 1 year).

3.3 *Group Composition, spatial distribution and habitat selection:*

I collected information on habitat parameters, group composition, and animal locations along two trails of c. 5.5 km and 9.5 km respectively; the trails were monitored once weekly. The trails were chosen in such a manner that, taken together, they ensured an almost-complete visual coverage of the study area: these trails followed ridge-crests on either side of which I sometimes had a visibility-range of up to 2 kilometres.

A group was defined as ≥ 2 tahr within 50 m of each other. Four social units were recognised based on the presence of age-sex classes: female groups, where adult females, small males, yearlings, or young could occur together; female-plus-young groups, where only females and either one or both the young classes were present; bachelor groups where only the large males occurred together; and mixed groups, where one or more large males occurred with a female group.

It was possible to assign each tahr sighting on the trail to one of twenty three 0.0625 km^2 cells on a system of grids overlaid on a 1:25,000 Survey of India topographic map. Later, for the purpose of relevant analysis, I collapsed data into grids of 0.25 km^2. I analysed spatial overlap using Schoener's (1968) index of resource overlap

$$O_{jk}=\frac{1}{2}\sum |p_{ij}-p_{ik}|$$

where O_{jk} is the overlap between social units j and k; p_{ij} is the proportion of social unit j occurring in grid i; p_{ik} is the proportion of social unit k occurring in grid i. This could be expressed as a percentage figure that ranged between 0 (in case of no overlap) to 100 (for complete overlap). I calculated degree of spatial overlap from the total number of groups in a cell, rather than the total number of individuals, in contrast to what was done by McCullough *et al.* (1989) and Miquelle *et al.* (1992). (This was done since distribution of animals in space was perhaps more a reflection of a group's, rather than the individual's choice.)

Apart from this, I also assigned each sighting to one of six habitat categories described below:

- ***Sholas* (SHL)** were stunted forests that typically occurred in small patches following stream-courses. They were dominated by dense woody vegetation, mostly stunted trees with dense canopies, and the ground cover being predominantly dicotyledonous and herbaceous.
- **Bluffs (BLU)** were massive sheets of granite, with average slope exceeding 40°. Here the vegetation was very sparse, consisting mostly of mosses and some annual grasses.
- ***Kurinji* Scrubland (KSL)** were dominated by *Plebophyllum kunthianum*. In addition, species such as *Ageratina adenophora* and *Chrysopogon zeylanicum* were also common. Terrain-wise, these happened to be areas that were rather steep and rocky.

- **Broken Grassland (BRG)** typically had a slope of greater than 35°, and consisted of open stretches of grassland interspersed with exposed sheets of rocks. Annual grasses like *Apocopsis wighti* and *Tripogon* spp., along with sedges and sedge-like species (*Carex* spp., *Eriocaulon* spp., etc.) constituted the dominant vegetation.

- **Rolling Grassland (RLG)** occurred on the wind beaten knolls at the higher elevations (>2000 m). These areas had a predominance of graminoid (Graminae, Cyperaceae, Eriocaulaceae) vegetation. *Eulalia* spp., *Chrysopogon zeylanicum*, *Ischaemum* spp., *Arundinella* spp. were the principal species. Other than these, species like *Pteridium aquilinum*, *Osbeckia lineolata*, *Cyanotis arachnoides*, *Anaphalis* spp., and *Leucas* spp. also occurred.

Additional information recorded on trails included details of group composition, dominant activity, and habitat parameters associated with the location of the group including elevation, slope (measured with an altimeter and a clinometer respectively), percent rockiness, distances to nearest cliff, shola and road (estimated). I used distance to nearest *shola* as a measure of risk from stalking predators, the tiger and leopard in particular, which are known to kill tahr (Rice 1984). Distances to nearest road were used as a measure of security (from predation) derived from human presence.

Data on habitat use, and use of individual habitat parameters was analysed according to group type, since these were assumed to reflect differences in the way groups used habitats than the sexes *per se*. Each sighting of a solitary animal or a group represented a sample. For the purpose of analysis, I combined solitary females with female-plus-young groups, and solitary males with male groups. Data on the males were few, and consistent between the months, and were hence combined for analysis. I used a χ^2 test to examine differences in the group use of habitat types. Since sample sizes for mixed groups were small, they were left out of this analysis. I examined for differences in the use of habitat variables that followed at least an ordinal level of measurement with a Kruskal-Wallis one-way analysis of variance (ANOVA) by ranks with social unit as the treatment variable. This was preferred to the parametric alternative since it was insensitive to measurement inaccuracies, and circumvented the assumptions of normal data distribution and homoscedasticity

(Zar 1984). Non-parametric multiple range tests (Siegel and Castellan 1988) were used to identify which of the groups differed significantly.

Since several of the habitat variables might have been related among themselves (as, for instance, might be expected between slope and rockiness), a principal components analysis (PCA) was done with the Pearson's product-moment correlation matrix as the input (Pielou 1984). Since some variables (e.g. distance to cliffs) had large ranges in their magnitudes, log-transformations (Zar 1984) were used to normalise it; other variables that did not show normal distributions were ranked, and since the rank scores were normally distributed, they were included in the PCA. Varimax (Norušis 1990) rotation method was used to determine the correlation of the habitat variables with the PCA axes.

3.4 *Forage availability and use*

Availability of forage in the KSL, BRG, and RLG habitats was estimated once in February-March. Random points were located on a 0.5 cm × 0.5 cm grid overlaid on a 1:25,000 topographic base map of the study area as detailed by Marcum and Loftsgaarden (1980). After locating myself at each of these random points, I placed four 1 × 1 m plots in four perpendicular directions, 20 m apart, and visually estimated percent cover species-wise. Species that made up less than 5% cover were combined as 'others' during analysis. In addition, mean height of each species was also recorded. Height and the percentage cover of each species were multiplied to arrive at a measure of forage volume, which was believed to reflect biomass better than percent cover, or height alone. In certain areas, the terrain hindered physical measurement of vegetation parameters; here, visual estimates of the proportion of graminoid and non-graminoid vegetation were made from a distance.

It was not possible to estimate use of forage species by the tahr. Although females were mostly tolerant of close observation, biases attached to the direct-observation technique (Monro 1982) across habitats precluded its use in quantification of animal-usage; males were nowhere so approachable as to enable direct observation of feeding. Since tahr is classified as grazer (Schaller 1970, Rice 1984, *pers. obs.*), I used the proportion of graminoid vegetation in a habitat to represent its 'quality', and absolute forage volume to represent 'quantity'. To examine the relationship between forage and habitat-use, I used a Page test of ordered alternatives (Siegel and Castellan 1988).

3.5 *Diet quality:*

Since no direct measures of dietary quality of the sexes were available, two faecal indices to dietary quality - percent ash and percent crude protein - were used.

Fresh faecal pellet groups were collected on a monthly basis from animals whose age-sex identity was ascertained. The pellets were oven-dried in field and stored air-tight in polythene bags. Later, they were again oven-dried in the laboratory at 65°C for 24 hours, and ground in a Wiley mill. Samples from pellets were analysed using the macro-Kjeldahl technique (Grimshaw *et al.* 1989). Samples were not replicated in this analysis owing to a paucity of time; I therefore assume experimental errors to be constant across samples.

Literature is full of studies on domestic and wild ungulates that both recommend (Klein 1965, Leslie and Starkey 1985, 1987, Renecker and Hudson 1985), and dissuade (Hobbs 1987, Robbins *et al.* 1987) the use of faecal nitrogen as an index of dietary quality. The merit of using faecal nitrogen in estimating dietary quality in wild herbivores lies in the positive relationship that exists between faecal nitrogen and dietary nitrogen; faecal nitrogen, in turn, is related positively to dry matter digestibility (Robbins 1983). Criticism has been that faecal crude protein is affected by secondary compounds synthesised by plants as defence against herbivores (Freeland and Janzen 1974). Secondary compounds are found mostly in browse species (Robbins *et al.* 1987), and tahr is mainly a grazer (Schaller 1970, Rice 1984, *pers. obs.*). Hence the validity of using this technique in estimating the dietary quality of Nilgiri tahr.

The second index of dietary quality was the proportion of ash in the faeces. This was used as it indicates the coarseness of forage in terms of its silica content (Robbins 1983); the ease of the procedure was an added incentive for its use. Estimation of ash content was done according to the procedure given by Allen (1989).

3.6 ***Activity Patterns:***

Large males, small males, and adult females were observed through the study to determine activity budgets. Scan sampling (Altmann 1974) of groups at five-minute intervals was used to determine proportion of animals engaged in a certain activity; I approximated it to the proportion of time spent in the activity. The activities of interest were feeding (including searching for, biting, or swallowing food), moving, resting (including standing and ruminating), vigilance, and social activities (sexual, agonistic, etc).

Since, samples for each point in the scan were unequal, data points were weighted by group size for each of the 24 half-hourly intervals (0630-1830h) during the day to determine proportion time spent in different activities. A Kruskal-Wallis ANOVA based on ranks was used to detect differences in the proportion of time spent by the different age-sex classes in different activities; multiple range tests were done as described earlier.

All statistical analyses, save for the Page test, were done on the SPSS/PC+ statistical package (Norušis 1990). For all statistical tests, actual P values are presented where appropriate, and tests are considered significant if $P \leq 0.05$.

4. RESULTS

4.1 *Group Composition:*

In the period of the study, sexual segregation was most evident in the months between February and April. This is reflected in the relative proportions of the tahr social units seen during these months (Table 4.1). 13% of all male sightings were of solitary animals.

Table 4.1. Monthly observations of Nilgiri tahr group types at ENP.

Month	Group Type (percent of sightings)				*n*
	Female-Young	Female	Bachelors	Mixed	
December	25.0	36.4	25.0	15.6	44
January	33.3	31.0	26.2	9.5	42
February	27.3	50.0	18.2	4.5	44
March	43.5	32.6	19.6	4.5	46
April	30.8	34.6	30.8	3.8	26

4.2 *Spatial Distribution:*

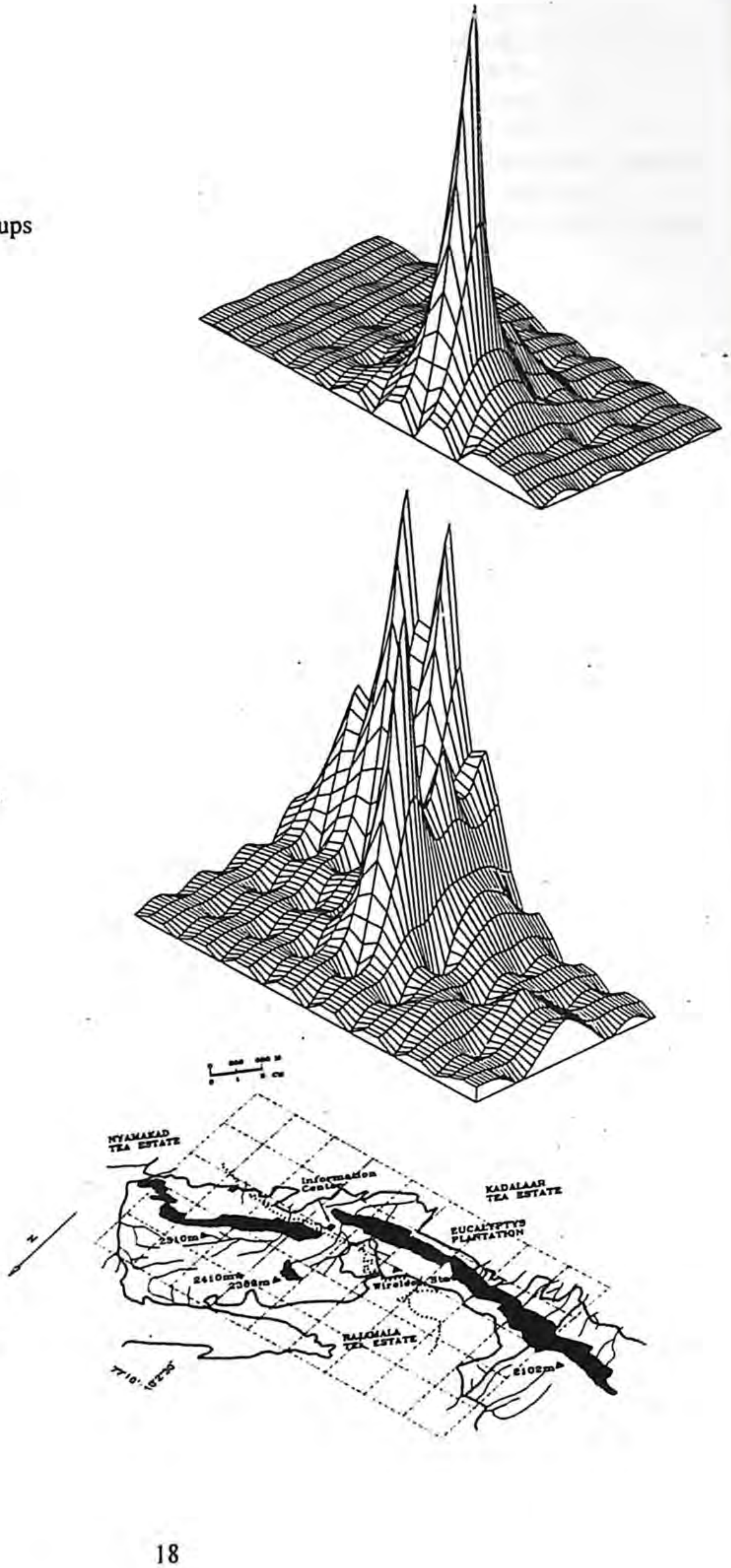
Males and females used different parts of the study area consistently through the study. Schoener's (1968) index of overlap, calculated for the degree of spatial overlap between bachelor groups and female groups (includes female and female-young groups), showed an overlap of 22.8%. A graphical representation of the intensity of use of different parts of the study area by male and female groups is given in Fig. 4.1. Males most commonly used the higher elevations and gentler terrain north and north-east of Naikolli Mala, whereas the females used the areas around the Information Centre and the Wireless Station most intensively.

Fig. 4.1 A graphical representation of the intensity of use of grid cells by bachelor and female groups.

Bachelor groups

Female groups

Grid/Base map



4.3 *Habitat Selection:*

The habitats classified *a priori* showed clear differences (Table 4.2). Bachelor and female units used habitats differently (Table 4.3). 80% of observations on large males in bachelor units

Table 4.2 Physical and vegetational attributes of the three habitat types in ENP (data from 44 random points).

Habitat Type	Elevation (m ASL)	Slope (°)	Rock (%)	Distance to cliff (m)	Forage Volume (cubic units/m²)	
					Graminoids	Non-graminoids
KSL	2065.3	25.1	23.4	112.3	556.2	782.5
BRG	1910.5	40.8	58.4	21.7	339.5	199.8
RLG	2121.7	18.5	1.8	249.8	636.5	190.2

were in Rolling Grasslands (RLG) alone, whereas females and female-young units were not that obligate to a single habitat type. They differed significantly in the selection of habitat for the overall duration of the study (χ^2=112.620, df=6, p=0.0000). Bachelor units used all the habitat types that

Table 4.3 Frequencies of tahr social units in different habitat types

Social unit	Bluffs (BLU)	*Kurunji* scrubland (KSL)	Broken Grassland (BRG)	Rolling Grassland (RLG)
Female-Young	9 (13.8)	32 (49.2)	22 (33.8)	2 (3.2)
Female	4 (5.3)	20 (26.7)	42 (56.0)	9 (12.0)
Bachelor	0 (0)	4 (8.5)	5 (10.6)	38 (80.9)
Mixed	0 (0)	6 (40.0)	2 (20.0)	6 (40.0)

- Figures in brackets are percentages
- Mixed units were omitted from the χ^2 test for differences in use of habitats by social units. (χ^2= 112.60, df=6, p=0.000)

female units used, except for the Bluffs which was used exclusively by the females and female-young units.

Bachelor, female and mixed units showed significant differences in the use of habitat components. Bachelor units used significantly higher elevations than did female or mixed units (Kruskal-Wallis ANOVA χ^2=85.02, p<0.0000), maintained significantly greater distances from nearest road (Kruskal-Wallis ANOVA χ^2=25.50, p<0.0000) than female, female-young, or mixed groups. They also kept greater distances from nearest cliff than females; mixed groups did not differ from bachelor groups in this respect (Kruskal-Wallis ANOVA χ^2=53.51, p<0.0000). Female groups used greater slope angles and higher percent rockiness than bachelor units, or mixed units (Kruskal-Wallis ANOVA χ^2=34.30 and 54.88 respectively, both p<0.0000). Bachelor groups and female with young maintained greater distances to *sholas* than female groups or mixed groups (Kruskal Wallis ANOVA χ^2=10.57 p=0.0143).

Several of these habitat variables were significantly correlated with each other (Table 4.4). This could potentially confound interpretations of the differences that might exist between the sexes

Table 4.4 A matrix of Pearson's correlation co-efficients depicting associations between habitat variables measured at 44 random points.

	Slope	Rockiness	Distance to nearest cliff	Distance to nearest shola	Volume of Graminoid forage
Elevation	-0.3251 p=0.016	-0.4628 p=0.001	0.3426 p=0.011	0.0078 p=0.480	-0.0745 p=0.315
Slope		0.7790 p=0.000	-0.5305 p=0.000	0.2336 p=0.063	-0.2651 p=0.041
Rockiness			-0.6684 p=0.000	0.3169 p=0.018	-0.2751 p=0.035
Distance to nearest cliff				-0.4751 p=0.001	0.0815 p=0.300
Distance to shola					-0.2555 p=0.047

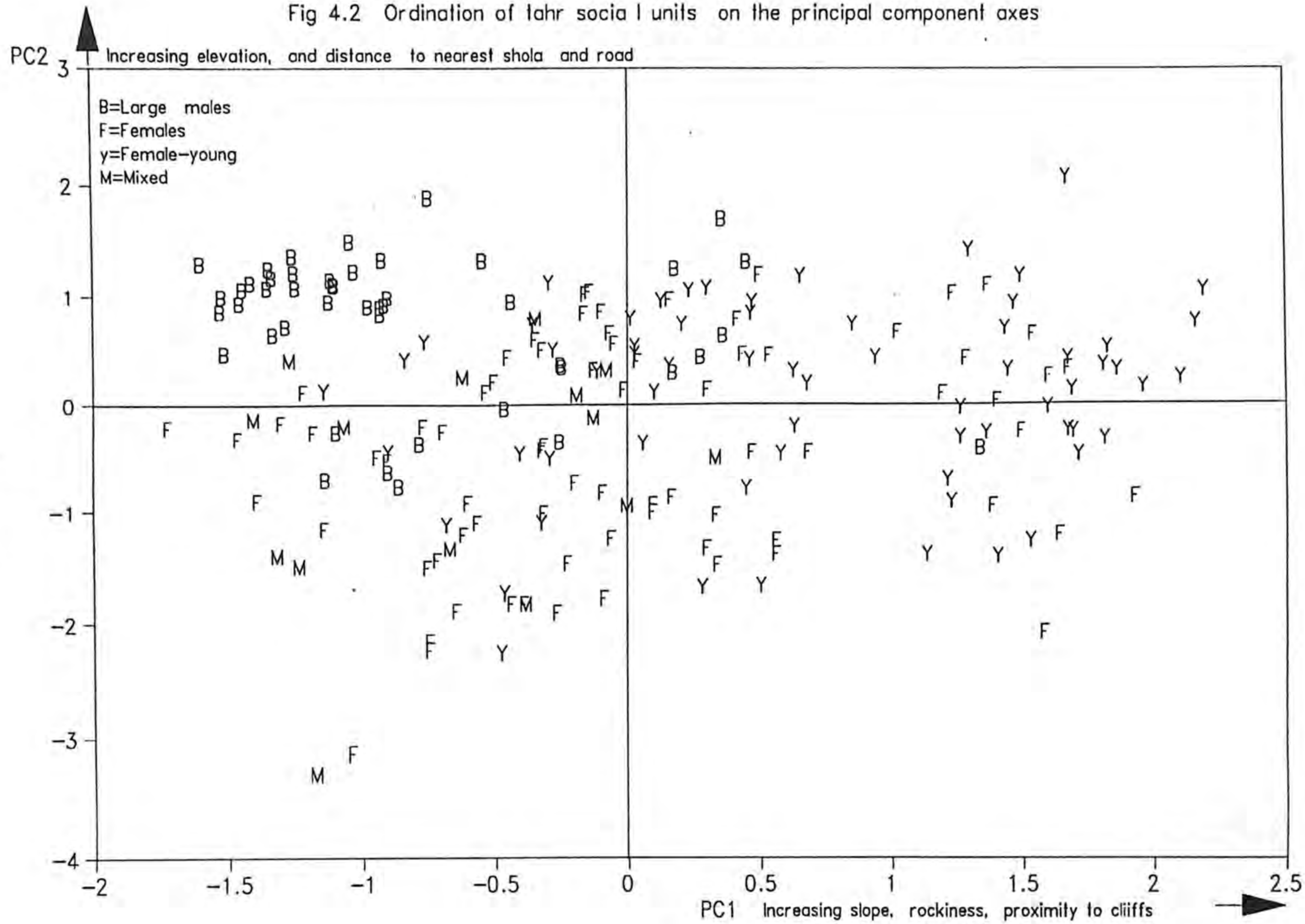
in the use of habitats. To examine the influences of each variable after removing the effects of other variables on it, a Principal Components Analysis (PCA) was used. Two principal components summarised 69.1% of the variation in the data set. The first principal component incorporated increasing slope, rockiness and proximity to cliffs, and decreasing elevation. The second principal component incorporated increasing elevation, distance to nearest road and nearest *shola*. Since assumptions underlying a PCA might have been violated to some degree, I made no statistical inferences from this analysis. The four social units were merely ordinated on these axes to represent different expediencies in habitat selection (Fig 4.2).

4.4 ***Forage availability and use:***

Measurements of forage availability were available only for three habitat types - BRG, SSL, and RLG. On the basis of natural history observations the tahr is known to be mostly a grazer. Therefore, I considered only the absolute volume of graminaceous forage, and its proportion relative to other forage in these habitats as variables of interest. RLG had a greater absolute volume of graminaceous forage than BRG, but was not significantly different from KSL (ANOVA $F=3.254$, $df=43$, $p=0.048$). RLG also had a higher proportion of graminaceous forage than SSL, but was not different from BRG (ANOVA $F=20.539$, $df=43$, $p=0.0000$). SSL had significantly greater volumes of non-graminaceous forage ($F=30.574$, $df=43$, $p=0.0000$) than either BRG or RLG.

No direct measures of use were obtained since feeding observations on tahr were not possible; neither was it possible to quantify vegetation features at the location of each tahr sighting. Correlations between the volumes of graminaceous and non-graminaceous forage, and proportion of graminaceous forage, with different habitat variables yielded results summarised in Table 4.4. To test the hypothesis that males were choosing areas of both higher graminaceous forage-volume and proportion of graminaceous forage, I predicted the direction of increasing male proportions *a priori* based on the above information on forage availability. Males showed an increasing tendency to form the bulk of the population with increase in proportion of graminaceous biomass (Page statistic $L=67$, $k=5$, $p<0.05$). In addition, from the correlations (Table 4.4), it can be observed that lower

Fig 4.2 Ordination of tahr socia l units on the principal component axes



slopes, less rockier areas, and areas farther from cliffs - typically the areas used by males - had higher graminaceous forage volumes.

4.5 *Dietary quality:*

The two indices of dietary quality used - faecal nitrogen and crude ash - did not indicate appreciable differences in the quality of diets of tahr of different age-sex classes (Fig 4.3). There was no difference in the faecal nitrogen concentrations between large males, small males and females ($F=0.00$, $df=80$, $p=0.999$); neither was there any difference in the percent crude ash in the diets of the above age-sex classes ($F=0.49$, $df=134$ $p=0.688$).

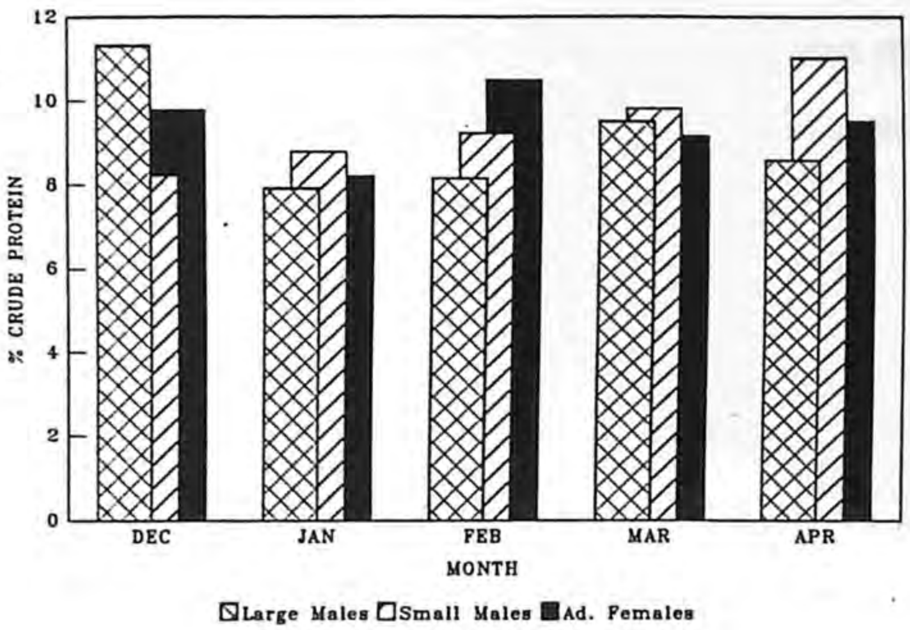
4.6 *Time-activity budgets:*

There were differences in the time-activity budgets of large males, small males, and females (Fig. 4.4). There was no significant difference in the time spent in feeding by the three classes (Kruskal-Wallis ANOVA $\chi^2=3.782$, $p=0.151$), or in vigilance (Kruskal-Wallis ANOVA $\chi^2=0.552$, $p=0.759$). Differences were observed in the time spent moving, resting, and in social activity (Kruskal-Wallis ANOVA $\chi^2=11.033$, $p=0.004$; $\chi^2=5.974$, $p=.050$; $\chi^2= 14.731$, $p=0.000$ respectively). Based on non-parametric multiple range tests, I found that females spent more time moving than the two male classes; larger males rested more than either females or small males; small males engaged in greater social activity (mostly fighting) than did females or large males.

Fig. 4.3 Measures of dietary quality

Variations in crude protein in
Nilgiri tahr faecal pellets.

(A)



Variations in percent ash in
Nilgiri tahr faecal pellets.

(B)

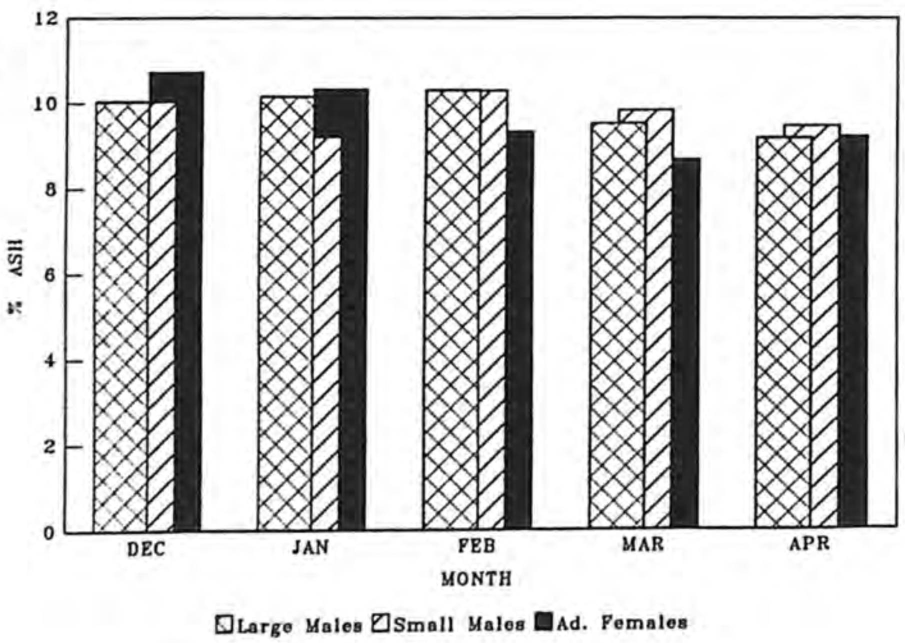
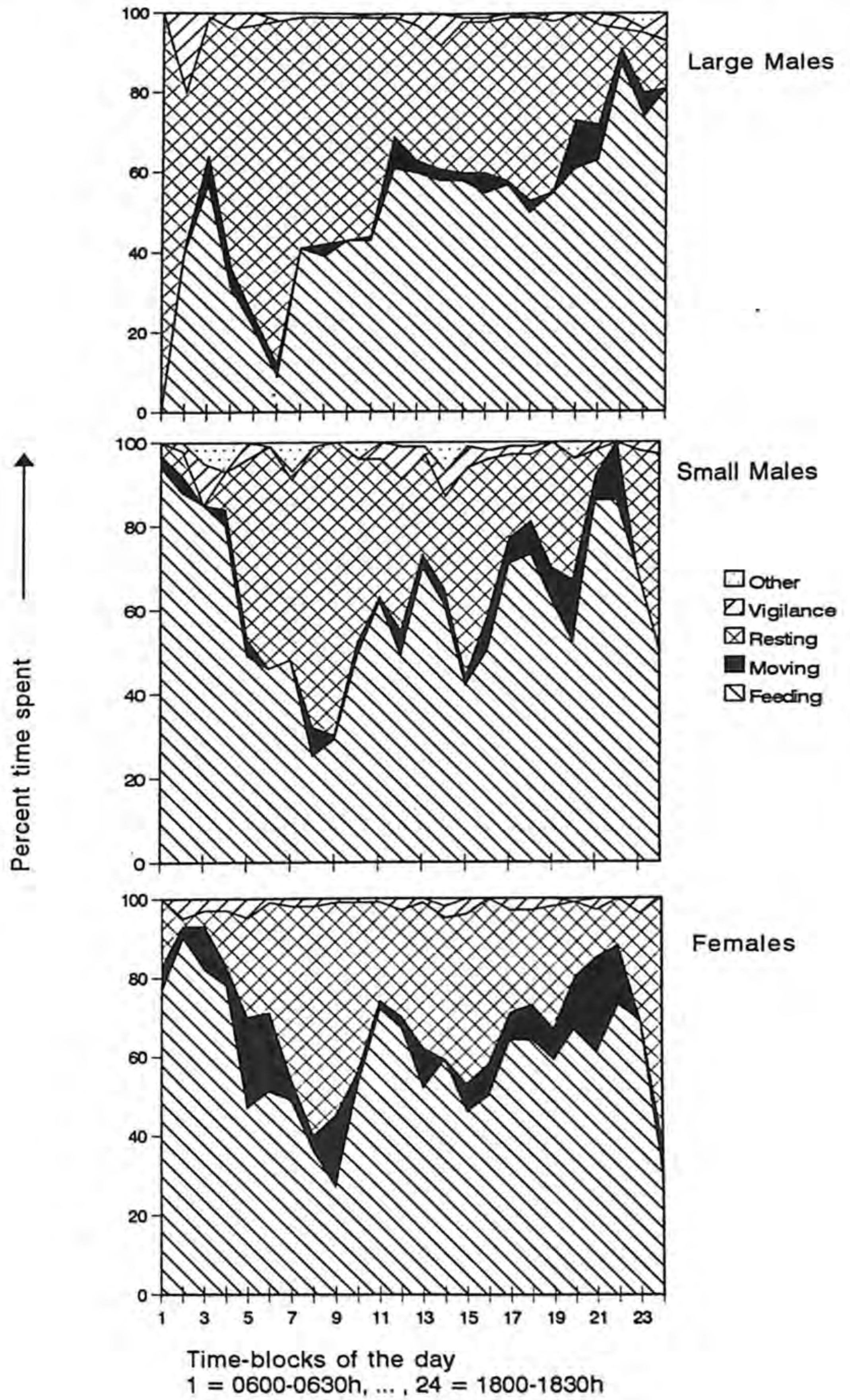


Fig. 4.4 Time-activity budgets of different age-sex classes of Nilgiri tahr.



5. DISCUSSION

5.1 *Introduction*

Are Nilgiri tahr sexually segregated? The findings of this study are equivocal on some aspects of tahr biology as regards the existence of sexual segregation, on some others, the patterns of segregation are clearly demonstrable. Large males consistently occurred in social units separate from female units (Table 4.1). Males and females differed clearly both in the use of space, and in the use of different habitat types (Fig. 4.1, Table 4.3). Spatial overlap (Schoener's overlap index = 0.228) between male and female groups was less than or comparable to the minimum figures of overlap between the sexes from other studies (McCullough *et al.* 1989, Miquelle *et al.* 1992). Males were practically restricted to areas at higher elevations that were characterised by the Rolling Grassland habitat - gentler, less rocky, farther away from cliffs, and richer both in terms of absolute and relative volume of graminoids. Females were relatively more catholic in the use of both physical space and habitat, in that they used areas and habitats (eg. BLU) where males were never found. Rocky terrain of higher slope angles (in BRG and KSL habitats) - typically areas that were closer to cliffs - seemed to be important to females in their choice of habitat (see Table 4.2 and Table 4.3). Males and females also differed in their patterns of activity (Fig. 4.4). Large males spent a greater proportion of their time resting than did either small males or females (Kruskal-Wallis ANOVA, χ^2= 5.974, p=0.050). On the other hand, females spent a greater proportion of their time moving than large or small males (Kruskal-Wallis ANOVA, χ^2= 14.731, p=0.000). There appeared to be a lack of segregation between the sexes as regards dietary quality (see Fig. 4.3) which I estimated using faecal protein (F=0.00, df=80, p=0.999), and crude ash (F=0.49, df=134, p=0.688). *Quality* alone is not likely to demonstrate all differences that might exist in the diets of the sexes.

5.2 *Theoretical predictions and empirical observations - some comparisons:*

5.2.1 *The Ecological Dimorphism Hypothesis:* Data from the study was in agreement on many predictions of this hypothesis. Before all else, it must be mentioned that this hypothesis assumes that areas superior in terms of offspring security, i.e. areas of relatively higher slope and rockiness, are necessarily not spatially identical with areas of higher forage biomass. Insofar as the situation at Rajamala is concerned, this assumption seemed valid (Table 4.2, 4.4). As studies on mountain ungulates have shown, areas with higher slope and percent rockiness are sites of higher security from predators (Geist 1971, Schaller 1977); so with the tahr at Eravikulam (Rice 1984, *pers. obs.*). Female-young units maintained greater proximity to the cliffs, i.e. areas of high percent rockiness and slope. They used BLU more often than did any other class of animals. The fact that the areas used more by females were poorer either in terms of absolute volumes of graminoids (in BRG), or in terms of lower proportion of graminoids (in KSL) (see Table 4.2), seems to validate the prediction made by Festa-Bianchet (1988) that security from predation is a consideration that overrides access to better forage. An interesting feature of Rajamala that encouraged female-use of certain RLG areas (as around the Wireless Station), was apparently the security from predators owing to human presence there; levels of predator activity were relatively lower in areas of human presence (*pers. obs.*). Taken together with the high availability of cliffs in these areas, human presence is likely to have added to the security-value of this area. The lack of asymmetry in quality of forage consumed is reflected in the constant values of faecal nitrogen, and ash both between different classes, and over time. As the season of births progressed, females-young groups moved into areas that were less rugged, and associated with the larger female groups (*pers. obs.*). Occurring in large groups, while offering the advantages of greater ability to detect predators (Jarman 1974), also allowed the females with young access to areas of better forage, as in the case of new flush of grass that followed the fires around the Wireless Station. Male areas, on the other hand, had very few of the attributes that could be regarded superior in terms of security.

As mentioned earlier, the Rolling Grasslands, where the males occurred, were superior to KSL and BRG both in terms of absolute and relative graminoid forage-volumes. Quantification of the differences in predation-risk on tahr in the male and female areas was beyond the scope of my study. Nevertheless, males seem to have offset the risk of predation to some degree by using areas where visibility was good; this however, was a feature that was hard to quantify. The positive direction of association between the proportion of graminaceous forage and the proportion of bachelor groups in the three habitats - KSL, BRG and RLG - also indicate that males might indeed be choosing areas that afford them a higher intake of choice forage, grasses. This choice, if fraught with risks of greater predation, is consistent with the *high risk-high gain* strategy observed in the case of bull elephants (Sukumar and Gadgil 1988).

5.2.2 *The Male Vulnerability Hypothesis:* In this case, depressed male body-condition following the rut is held responsible their differential vulnerability to predation. I had no means of ascertaining objectively whether large males were in a poorer body-condition following the rut; but my impression was that they indeed were. If male security from predation drives segregation, it is justified to expect male-areas as being relatively predator-free. But this was not the case. All but one of the four leopard scats, and all the dhole scats collected in the study area were in male areas. On the contrary, this suggests that males used areas associated with higher levels of predator activity. This is inconsistent with the findings of Morgantini and Hudson (1981) in the bighorn sheep, and Miquelle *et al.* (1992) in the moose, which indicated male use of areas with lower predator activity. However, it must be stated that males enjoyed far greater visibility in these areas than elsewhere. The tendency of males to associate in large groups (of up to 43) might also have offset this concern. As argued in the preceding hypothesis, habitats selected by females were superior in terms of security. Thus, if predation constrained male use of habitats, predictions of this hypothesis state that they should have used the same areas as females non-synchronously. Since this did not occur, male selection of habitat in tahr might not have been cued to predator presence, or rather, the lack of it. Hence, my findings do not support the predictions of this hypothesis.

5.2.3 *The Sexual Size Dimorphism Hypothesis:* The essence of this hypothesis is that habitat parameters of importance are distributed unequally across habitats, and there exist body-size-related differences in the requirements of the sexes, which can be met by using the habitat that best matches the sex's need. The fall-out of such a difference in the selection of habitats, in terms of physical space, forage, and activity patterns associated with their use, would manifest as sexual segregation.

As mentioned earlier, there exist significant differences in the relative and absolute volume of graminoid forage between habitats. Body-size considerations predict that, all other things being equal, males, which are about 70% larger than females (F. B. Swengel, *unpubl. data*) need greater absolute amounts of forage to meet their metabolic needs (Kleiber 1975, Eisenberg 1981). In this regard, choice by large males of habitats offering greater graminoid forage-volume is consistent with the prediction that they will do so. However, information from activity budgets of the age-sex classes reveal non-significant differences with reference to percent time spent feeding. Conceivably, the ways in which energetic requirements of males could be met, given equal feeding times, is by increasing bite rates, or bite sizes (White 1983), or minimising expenditure of energy. While there is no data on either bite rates or bite sizes in tahr, I found that large males minimised expenditure of energy by resting more, and moving less than females or small males (differences *w.r.t.* resting only). This implies that even if the total time spent feeding were the same, males would be able to meet more of their requirements as their expenditure in energy is less. Patterns similar to this have been found in the moose, *Alces alces* (Miquelle *et al.* 1992). I was unable to find studies that measured seasonal energy requirements of males and females in caprids. But, Clutton-Brock *et al.* (1982), estimate the absolute energetic cost of the rut in the red deer *Cervus elaphus* stags to be greater than the cost of gestation and lactation in hinds. Since there are no costs of growing antlers and territory-maitenance (like roaring) in the tahr, as in the red deer, I have assumed males and females have similar absolute energy requirements.

As mentioned earlier, feeding for the same time as the females, males might be meeting their higher absolute metabolic needs by resting more, and moving less than females. But it does not explain why the sexes show such clear spatial segregation. This question can be split into two components:

a) Why do males occur in the habitats that they do?

Absence of differences in dietary quality of animals of different age-sex classes can be conjectured to mean an absence of differences in the forage quality in areas they choose, assuming males and females are free to choose the forage they want. The quantity of forage in male areas is greater, but again, males do not seem to be availing the concomitant benefits of this inequity, since they spend the same amount of time feeding as females and small males. Variation in bite size might still allow higher intakes in males, while this is something they could do in female areas as well. But, males do *not* occur there. If males do *not* derive any *benefit* from occurring in these areas, it suggests that there are substantial *costs* attached to the use of female areas. The explanation to this might well hinge on the way resources are distributed in the male and female areas. Patchiness of food can be expected to be greater in rockier female areas. Costs attached to the utilisation of a resource distributed thus might well entail an increase in the proportion time males spend moving, which is an added *cost*.

b) Why don't females occur in the same areas as males?

I am unable to explain this based on body-size considerations. If the male occurrence is due to a more equitable distribution of forage (which allows them to utilise it with minimum energy expenditure), there is no reason, based purely on body-size considerations, that can explain why females do not occur there as well.

So, the answer to this question might well be that females *are females*; they are constrained by concerns beyond body-size, the paramount one being offspring security. A behavioural explanation based on body size - that larger-bodied males exclude females from 'male' ranges - could explain differences in spatial distribution. Such a thesis, in the absence of supportive data, should be regarded as merely speculative.

Based on my data, I propose that sexual size-dimorphism does not explain spatial segregation in the Nilgiri tahr. This might be true based on energetic considerations. When factors like unit body-weight requirements of important minerals such as calcium (Robbins 1983), and their distribution in space are considered, spatial segregation might be better explained by size-dimorphism.

5.3 *Evolutionary history of the Nilgiri tahr and sexual segregation.*

Taking its origins in the temperate latitudes that are characterised by a distinct seasonality in the availability of primary resources such as forage, the ancestor of the tahr colonised tropical latitudes during the last glacial epoch. In the process, it radiated into the Nilgiri (*Hemitragus hylocrius*), the Arabian (*H. jayakari*), and the Himalayan (*H. jemlahicus*) tahr respectively (Schaller 1977, Geist 1987). Following the glacial melt, areas the Nilgiri tahr occupied began to regain their tropical qualities. The Nilgiri tahr were conceivably pushed into areas that maintained a "temperate" nature within this tropical latitude - a factor that might be largely responsible for the patchiness of the Nilgiri tahr's present distribution.

Sexual segregation, almost a norm with the ungulates of the northern latitudes (Peek and Lovaas 1968, Geist 1971, Cameron and Whitten 1978, McCullough *et al.* 1989, Weckerly 1993, Koga and Ono 1994), is believed to be adaptive in such seasonal environments, by reducing intra-specific (inter-sexual) competition during the seasons of resource shortage (Geist and Petocz 1977, Beier 1987). The tahr takes its origins in such an environment, but now finds itself in a different environment where such a trait would presumably be of neutral adaptive value owing to a less variable distribution of food between seasons. By virtue of this unique evolutionary-geographic position, the tahr is an interesting species in which to examine the extent to which previously-adaptive traits persist in *neutral* environments. Geist (1981) discusses the case of the relatively-tropical desert bighorn sheep as an animal with "less-than-perfect" adaptations that evolved in response to the temperate environment of its origin, but has now been *left behind*. Could this well be the case with the Nilgiri tahr with reference to sexual segregation?

5.4 *Conclusions*

In conclusion, sexual segregation occurs in the Nilgiri tahr, in its most obvious form as spatial segregation. Identification and measurement of subtler modes of segregation were beyond the scope of this study. Based on the above discussion, the Ecological Dimorphism hypothesis seems to explain segregation in the tahr best; the Male Vulnerability hypothesis and the Sexual Size-Dimorphism hypothesis do not seem tenable in the context of the Rajamala tahr.

Sexual segregation can be best understood with studies that cover the animal's whole annual cycle. Important answers lie in identifying *points of change* in the distribution of animals temporally, and associating them with temporal changes in habitat parameters of importance.

The review of current hypotheses that explain sexual segregation (Chapter 1) reveals that most regard sexual segregation as a *strategy*. Here, one study on the sexual segregation of wintering hooded warblers *Wilsonia citrina* deserves mention. It demonstrates the existence of sexual segregation based on simple environmental cues such as the habitat differences in the direction of stem-branching (Morton 1990). This might be a proximate explanation for sexual segregation, and its applicability to larger mammals is certainly open to debate. But, it certainly is a caution on over-emphasising heuristic interpretations of biological phenomena, be it sexual segregation, where disparate features of an animal's biology are pigeon-holed into logical constructs.

5.5 *Sexual segregation - has it any management value?*

The contradiction, or validation of the above theoretical predictions, does not directly provide information that can be translated to management actions. Nevertheless, the findings of this study further confirm the existence of distinct differences in the way the sexes use resources.

With specific reference to the Nilgiri tahr, males and females are shown here to differ distinctly in their choice of space. Knowledge of such differences should encourage management to formulate conservation strategies for species, bearing in mind these differences, and how sexes might be differentially affected by inputs of the management. Assuming applicability of the results of this study to tahr populations elsewhere, plantations of exotic fuel- and pulp-wood species

(*Acacia mearnsii*, *Eucalyptus* spp. and *Pinus* spp.) in several areas in the tahr ranges, for instance, might have differentially affected males who, we know as using the rolling grassy downs - favoured area for plantations - more than the females. Similar discretion should be employed in using 'tools' of management, like fire, since it might affect sexes differentially.

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