DETERMINANTS OF BUTTERFLY SPECIES DIVERSITY: PLANT DIVERSITY, FOLIAGE HEIGHT DIVERSITY, AND RESOURCE RICHNESS ACROSS VEGETATION TYPES

DISSERTATION SUBMITTED TO SAURASHTRA UNIVERSITY,
RAJKOT,
IN PARTIAL FULFILMENT OF THE MASTER'S DEGREE
IN WILDLIFE SCIENCES
JUNE 1999

BY
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UNDER THE SUPERVISION OF
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CERTIFICATE

This is to certify that the dissertation entitled "**Determinants of butterfly species diversity, plant diversity, foliage height diversity, and resource richness across vegetation types**" embodies a piece of original research work carried out by Mr. Krushnamegh Kunte for the partial fulfilment of M. Sc. (Wildlife Science) degree of Saurashtra University Rajkot. The research work was carried out under my supervision at the Wildlife Institute of India during November 1998 to June 1999. I also certify that this work has not been submitted for any other degree of any University.

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Dated: June 20, 1999 **(G.S. Rawat)**

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MARATHON ACKNOWLEDGEMENTS

All the faculty members at the Wildlife Institute of India (WII) have helped me in one way or the other, but I take special pleasure in mentioning two. Dr. Gopal S. Rawat knows natural history of plants so well that I succumbed to his project supervision, than of others, as my way of respecting a person. He is a naturalist who initiated in me thinking about plants and their ecology. He has been the most cooperative and considerate person I met in the last two years. Dr. Y. V. Jhala, M.Sc. Course Director, was responsible to force me into narrowing down to a specific topic for M.Sc. dissertation, which helped tremendously. I shall remember him because he was a good teacher. And above all, he reminds me of something. Didn't someone say that science is not about nice statistics but about great ideas?

Present and ex-students/researchers at WII, Centre for Ecological Sciences (CES) and National Institute for Advanced Studies (Bangalore)- M. D. Madhusudan, Charudatta Mishra, Shomita Mukherjee, Robert John, T. R. Shankar Raman and Dr. Venkatachalam Suri, went through the proposal and rough drafts of the thesis, and with them I had fruitful discussions.

In WII, often my only refuge was its wonderful library. The library staff- from top to bottom, was so helpful and informal in everything I required of them, that I almost included them in my friend circle at WII.

In Bangalore I was hosted for a while by Mallapur family, and in Pune by Rao family, which was enjoyable. At CES, Utkarsh Ghate was there to help in all his capacities- plants, logistics, advice, data analysis, discussions, anything and everything any time. And it seems his capacities are growing rapidly! He has been an enjoyable company throughout. Srinidhi was patient with my viruses and helped with the computers. Sivan, Harish Bhat and Suresh identified plants and worked through plant-related material. I also thank K. A. Subramanian,

E. Kunhikrishnan and Nutan Pisolkar for their help. Dr. Niranjan Joshi has been consistent in making me see my way through deep slush of raw, wild ideas to presentable theory.

The field work was made possible and enjoyable through active co-operation by staff of the Forest Department of Tamil Nadu. I especially thank Mr. R. P. S. Katwal (Chief Wildlife Warden, Tamil Nadu), Mr. S. K. Srivastava (Wildlife Warden, Indira Gandhi National Park and Sanctuary), and Mr. A. Nagarajan (Range Forest Officer, Ulandi Range, Top Slip). Canopy sampling was an important component of my field work. Mr. Ashok Captain and Mr. Ajay Tambe, Pune, taught me climbing and gave very useful tips on tree climbing, besides providing some climbing equipment. Without their initial help, climbing would have been impossible. I had learnt some jungle craft from Ketan of Theppakadu- a hard core Kuruba, and it was further developed by Ganesan of Irumapparai- a Kader by soul and body. His guidance through the seven months of the field was a great asset. The people of Anamalais, notwithstanding the big language barrier, cannot be forgotten, for they made my work easy and the life very comfortable. Plus they tolerated my uninterrupted singing of Lata, Asha, Kishore and Talat!

This project was financially supported by, in the alphabetical order, the Centre for Ecological Sciences (Bangalore), the Life Research Foundation (Pune) and Wildlife Institute of India (Dehra Dun).

And now, some things that are rarely acknowledged in print, but have deepest influence on a person's thinking and life. Behind a researcher is a person and a person is moulded by other persons. They enrich his environment, his thinking, his imagination, his dreams and his work. Since such a luxurious space as is present here on this page is rarely allowed to acknowledge so diverse a people in so profuse a word, I might as well exploit it. A few persons had nothing to do directly with the thesis, but have influenced me in more ways than one. I learnt, am learning, so much from Prof. Madhav Gadgil (CES), just as Ekalavya learnt from Dronacharya. The ecologist-conservationist who has formed such a giant of character; and such a controversial figure that people love him, people hate him, but he influences everyone. Prof. Anil Gore (Head, Dept. of Statistics, Pune University) taught our class statistics, all right, but we could have learnt that from many other people. What he has taught me about my future profession and life in general, could have hardly been learnt from others.

They said I have always been a day-dreamer. Yes, it is due to several places and people who shared my past, and will share my future. Vateria, Hopea, Calophyllum- thanks for what you are, where you stand, and the way you stand. Niranjan Shukla, Ajit Jogalekar, Aadish Dani, Shailesh Deshpande and Sameer Sahasrabuddhe are my friends, apart from others mentioned here, with whom I grew and developed. Sameer Kulkarni because of whom I started watching and liking stars; and The Little Prince because of whom I started loving them. These are two persons with whom I spent innumerable nights outdoor- the nights of glittering stars and silent moonsets. To beat the rest, there are always Kumar Gandharva, Bhimsen Joshi, Amjed Ali Khan, Shobha Gurtu……and Beethoven wrote Eroica, the 5th, Pastoral, the 9th; Tschaikowsky- Pathetique; Mozart's Arias, Schubert- Unfinished, Great C Major; These are angels who blur my vision of "real world"- so often! Joseph Haydn started it, and Herbert Von Karajan conducted it all; why blame me for what I am?

SUMMARY

MacArthur and MacArthur's (1961) theory of foliage height diversity, which was originally discussed as a determinant of bird species diversity, has been a strong concept describing the possible role of vegetation structure in deciding resource use, habitat selection and diversity of organisms. They measured foliage profile, and calculated foliage height diversity using information theory. Their results showed increase in foliage height diversity from simple to complex vegetation types, and bird species diversity was positively correlated with it. They then proposed an evolutionary mechanism to explain this correlation. A continuous flow of studies on vegetation structure and species diversity or habitat use of organisms followed after MacArthur and MacArthur (1961), but mostly they focused on birds. Subsequently, vegetation parameters other than foliage height diversity, such as horizontal vegetation heterogeneity or patchiness, also proved equally useful or better predictors of bird species diversity. Moreover, some studies revealed that foliage height diversity and bird species diversity were not correlated in a few cases. This brought forth a question whether or not foliage height diversity is a strong determinant of bird species diversity, or a frequent correlate of some other factor that has a strong influence on species diversity.

To find out why in some cases MacArthur and MacArthur's (1961) theory did not explain species diversity, I identified following assumptions in their theory, which were unstated in their paper: i)resources for a species are evenly dispersed within a horizontal vegetation layer, ii)resources are unevenly dispersed across the horizontal layers, iii)even for generalist species, the cost of switching over between layers is high, which would preclude switching over between layers, and iv)if the first three assumptions are true, then each horizontal layer of vegetation would have a different set of species, each layer adding a

similar magnitude of diversity in more complex habitats. If these assumptions do not hold true for real biological communities, one would expect that foliage height diversity would not be a good predictor of species diversity in all situations. To test MacArthurs' assumptions and explore patterns of butterfly diversity across vegetation types, I studied butterflies at the Anamalais, southern Western Ghats, in southern India. I sampled foliage height diversity in vegetation plots and butterflies on count lines as well as all-out-walks (opportunistic sampling), recorded body measurements of the butterflies, floral parameters of the plants on which the butterflies fed, and compiled information on larval and adult feeding plant resources. Using these data, I tested three possible determinants of butterfly species diversity, namely, 1.foliage height diversity, 2.plant species diversity, and 3.resource richness in different vegetation types. This was probably the first attempt to analyse growth form-wise resource richness and utilisation by butterflies across vegetation types, in the light of foliage height diversity theory.

Although the correlations between butterfly species diversity, plant species diversity and foliage height diversity were statistically significant, the butterfly species diversity was not perfectly correlated with these two determinants. Butterfly species diversity increased from grassland to deciduous forest, through shrub savannah and teak plantation, but was less in the mid-elevation evergreen forest as compared to the deciduous forest. Plant species diversity and foliage height diversity, on the other hand, increased from the grassland to the evergreen forest, with the deciduous forest falling before the evergreen forest. The resources for butterflies were not distributed in the vegetation types as assumed by MacArthur, and butterflies were not observed following the pattern of habitat or resource utilisation as predicted by the theory. As a result, foliage height and plant species diversity did not satisfactorily explain the butterfly species diversity. However, larval host plant and total plant resource richness correlated significantly and appropriately with the butterfly species diversity. Therefore resource richness seems to be an appropriate and better predictor, or at least a correlate, of butterfly species diversity in situations when other predictors may not be correlated with it.

This study suggests that butterfly species diversity is dependent more on the resource diversity. However, foliage height diversity and plant species diversity need not be satisfactory surrogates for resource diversity in all situations. Therefore butterfly species diversity may vary independently of plant species and foliage height diversity. Another important result of this study was that even for butterflies, which are directly dependent on plants, the resource richness is not necessarily correlated with the plant species diversity. It means that butterflies selectively use certain plant resources more than other plant resources. I speculate that it would be underlying utilisable chemical diversity and "sociability" of plant resources used that would ultimately decide butterfly species diversity within a vegetation type. I define a "sociable host plant" as the one that supports many insect "guests". The butterfly assemblages using plant resources with maximum utilisable chemical diversity and sociability would be most diverse in the vegetation type supporting these sociable host plants. However, sociability of the utilisable plant species, and resultant butterfly diversity, may be independent of total plant species diversity or foliage height diversity in the vegetation type.

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DETERMINANTS OF BUTTERFLY SPECIES DIVERSITY: PLANT DIVERSITY, FOLIAGE HEIGHT DIVERSITY, AND RESOURCE RICHNESS ACROSS VEGETATION TYPES.

1. INTRODUCTION : Patterns and causes of dispersion of life forms across vegetation types, in space and time, have been the ever-exciting issues among population and community ecologists. This has also been among the most important themes in studies related to biodiversity. Although the patterns of species distribution are governed potentially by very many biotic and abiotic factors, ecologists have been trying to figure out and explain role of the most important factors.

Among such factors is perhaps the vegetation structure. Robert MacArthur and John MacArthur (1961) theorised it in terms of foliage height diversity. In brief, foliage height diversity is a measurement of distribution of foliage in horizontal layers in a vegetation type. Foliage height diversity could be calculated using some diversity index, and MacArthur and MacArthur (1961) used Shannon's diversity index. Thus, a grassland which has all the foliage restricted to a single layer close to the ground has low foliage height diversity. Progressing through savannah, scrub, deciduous forest and tall evergreen forest, one encounters a gradual increase in height of the vegetation, and subsequent increase in amount of foliage in different height classes (horizontal layering of the foliage) which corresponds to herbs, shrubs, small trees and large trees. This is a simplistic view, but gives a rough idea of structures of the vegetation types. Thus, there is corresponding increase in foliage height diversity from single-layered to multi-layered vegetation types. Based on whether the vegetation types have single or multiple layers, they can be classified as simple or complex habitats. Although there is a continuum of complexity, it is easier to understand the arguments when dichotomy is used, therefore it will be used here whenever required. It is a simple empirical observation that one encounters relatively less number of species of plants or animals in simple habitats than in complex habitats. Although this pattern is very intuitive due to over-familiarisation, it was not given much theoretical treatment. In 1950's other ecologists, such as Elton and Miller (1954), also were thinking in terms of classifying the habitats in structural entities and looking at diversity patterns, but it were MacArthur and MacArthur (1961) who first gave it a formal theoretical framework. Their study on birds in Florida, Panama, Pennsylvania and Vermont showed a significant positive correlation between foliage height diversity and bird species diversity, and the residual variation was not explained by additional data on plant species diversity. Although in the same paper they agreed that their results were only statistical, they proposed an evolutionary mechanism by which foliage height diversity would govern bird species diversity. Their argument goes on the following lines:

“A large number of species can be accommodated in an environment in a variety of ways of which there are two extremes. Each species may have different habitat preference and feed throughout this habitat on all kinds of food, or, all species may share the entire habitat, each species feeding on a different variety of food or in a different situation within the habitat. The first extreme violates what might be called the “jack of all trades- master of none” principle that natural selection favors the increased efficiency resulting from a certain amount of specialization. In the other extreme, specialization has proceeded so far that time and energy are wasted in travelling between spots for which the specializations are adapted. It is hard to say just where the balance of these opposing requirements would be reached, but it is clear that greater specialization resulting in increased efficiency would always be favored as long as no time and energy are wasted. And no time or energy will be wasted if niches are “convex” in the sense that between any two fairly distant feeding places there will be a fairly natural route also consisting of feeding places. A specialization to a single tree species in a mixed forest would clearly violate this since, in passing from one suitable tree to another, the bird would go through many unsuitable ones. Thus, natural selection would tend to eliminate a situation in which bird species diversity depended upon tree species diversity, unless, as in some fruit eating species, a very remarkable improvement in efficiency is achieved along with the restriction in feeding position. Thus, one principal result of these censuses can be predicted on assuming that niches are convex." (MacArthur and MacArthur 1961, p.597).

Many studies on vegetation structure and species diversity followed MacArthur and MacArthur (1961). The focus has been mainly on foliage height diversity alone (e.g. MacArthur *et al.* 1962, 1966, Murdoch *et al.* 1972, Cody 1975, Daniel 1992), but soon ecologists tried other habitat parameters, along with foliage height diversity, or different ways of measuring them. For example, Oriens (1969), Rotenberry and Wiens (1980), Roth (1976) compared horizontal patchiness- "heterogeneity", and foliage height diversity in predicting bird species diversity. Willson (1974) compared percent vegetation cover in different layers with foliage height diversity. These studies provided a positive correlation between foliage height diversity and species diversity, but in some cases heterogeneity proved to be a better predictor than foliage height diversity (Roth 1976). However, some did not show positive correlations, or very weak correlations, between foliage height diversity or other habitat structural parameters and species diversity (August 1983, Daniel 1992, James and Wamer 1982, Pearson 1971, Tomoff 1974. MacArthur (1964 and 1965), and MacArthur *et al.* (1966) mentioned that foliage height diversity had relevance mostly in the same vegetation types, and that aquatic ecosystems were an exception. Foliage height diversity was not successful or sufficient while comparing deciduous vs. evergreen or coniferous vs. angiosperm forests. Anderson and Shugart (1974), and Pearson (1971) showed that birds respond to presence of specific tree species or their densities, rather than habitat parameters. Pianka (1966, 1975) discussed habitat heterogeneity, resource dispersion and richness, and resource utilisation by desert lizards, and how all this would affect niche space and speciation. Unfortunately, none of these studies actually quantified resource richness and resource utilisation across the gradients of habitat and foliage height diversity. Due to conflicting results in different areas or by different researchers, there have been some difficulties in generalising the trends from studies on habitat structural parameters and species diversity (see Willson 1974).

Studies and discussion on effects of vegetation structure on animal diversity and habitat use had concentrated more on birds and lizards as model groups (Cody 1985, Pianka 1966, 1975). However, both these animal groups are predominantly insectivorous, not directly dependent on plants. Therefore relative roles of plant species diversity and vegetation structure could not be directly tested by using these groups. Moreover, studying and quantifying resource utilisation and resource richness, the two factors that are likely to influence habitat perception and utilisation drastically, is very difficult for insectivorous groups. This cannot be done without dissecting specimens for analysing gut contents, and without facilities for captive conditions to aid careful observations, which may alter behaviour of the animals. Given these problems with birds and lizards, insects, particularly butterflies, seem much better choice. Quantifying their habitat use is straightforward. Their resource utilisation can be studied in the field without disturbing them. Taking their body measurements, quantifying resources and resource richness also is easier. In spite of these advantages, insects have been ignored during previous studies on this subject. There have been many studies dealing with plant architecture and insect species diversity (Lawton 1983, Strong *et al.* 1984), but these concentrated mostly on a few plant species and how they affected diversity of phytophagous insects. Investigations into wider community-level patterns of habitat use, food resource use and richness were lacking, which this study tried to accomplish.

The basic objective of my study was to explore pattern of butterfly diversity across vegetation types, and to study resource utilisation of butterflies. Using this, second objective was to test the assumptions and argument of MacArthur and MacArthur (1961) with help of butterfly communities, and try to find out why the studies based on this theory did not yield consistent results. As is revealed and explained in later sections, the butterflies did not seem to use the vegetation types and resources in ways assumed and/or predicted by MacArthur and MacArthur (1961). The theory, therefore, did not explain satisfactorily butterfly species diversity across vegetation types.

2. MATERIALS AND METHODS :

2.1.Study Area: The field work was carried out in the Indira Gandhi National Park and Wildlife Sanctuary situated 80 km. away from the Coimbatore city in the southern Indian state of Tamil Nadu. The sanctuary lies in the Anamalai hills, on the eastern side of the southern Western Ghats, south of the Palghat gap. It covers an area of 955 km^2, and presents a diverse array of vegetation types and altitudes. It rises from 300-odd metres to more than 2,400 m. above m.s.l., harbouring natural scrub, deciduous forest, moist mid-elevation evergreen and shola forests, mid- and high-elevation grasslands, and teak plantations. It also has some human-influenced vegetation types, such as the bamboo forest and shrub savannah, both are maintained by fire. All this results into a rich landscape with immense habitat diversity for butterflies.

2.2.Vegetation Types: In all, five vegetation types were sampled during butterfly counts, namely, 1.high-elevation grassland, 2.shrub savannah, 3.teak plantation, 4.mixed deciduous forest, 5.mid-elevation evergreen forest; and three more- shola forest, bamboo forest and scrub, were occasionally visited.

1.High-elevation grassland: this is a naturally occurring grassland above 1,800 m., and present in Tamil Nadu side of Anamalais only at the Grass Hills World Heritage Site. The vegetation is composed mostly of short grasses and herbs, about 0.1 to 0.2m. in height. Asteraceous herbs are most common. The grasses may be in clumps, but many herbs usually grow in small clumps. Dominant grass species include *Chrysopogon zeylanicus, Eulalia thwaitessi, Andropogon* sp., and *Themeda triandra*, and herbs- *Lucas* sp., *Erigeron, Emilia sonchifolia*. Occasional dwarf shrubs are present, but none over 0.5m. in height. In deep valleys the evergreen forests ("shola", see below) may be present. March and April are the only dry months, precipitation in other months in form of rain or dew is considerable.

2.Shrub savannah: this is a secondary vegetation type. Originally it must have been a scrub or stunted deciduous forest, but is now maintained as a tall-grass (up to 2m. tall) savannah by uncontrolled fires initiated by local people from surrounding villages. As a result, fire-resistant bunch grasses such as *Cymbopogon flexuosus* and *Themeda cymbaria* have dominated the vegetation. *Phoenix* also is abundant. Most of the species have a short growing season- only the monsoon and immediate post-monsoon months, and vegetation remains dry for rest of the year, i.e. between January and April.

3.Scrub: at the foot of the ghats and towards Thekkady Wildlife Sanctuary in Kerala is a natural scrub vegetation that I visited occasionally. The area is covered with thickets of various species of *Acacia* and *Capparis*, with short grass and herbs for the ground cover. In slightly moist places *Bambusa arundinacea* and other deciduous trees such as *Schleichera oleosa* and *Cassia fistula* grow. The vegetation is more or less stunted, attaining a height of about 10-15m. on an average.

4.Teak plantation: the teak plantation at Cheechalai is about 30-year old single species tree stand that is maintained more or less clear of natural tree regeneration. The undergrowth is composed of exotic *Chromolaena* and indigenous weedy species such as *Sida rhombifolia*, *Desmodium*, *Pueraria*, etc. Little grass and small bamboo clumps are occasionally present. The plantation has some rare individuals of a handful of indigenous trees, among which are mostly *Lagerstroemia parviflora*, *Cassia fistula* and *Wrightia tinctoria*. The average height of the teak trees in this plantation is slightly over 25 m.

5.Bamboo forest: area between Top Slip and Kozhikamudhi elephant camp must have been previously exploited either for timber extraction and/or selective bamboo growth. Since the rainfall is heavy, the area was disturbed earlier, and now gets burned once in a few years, it is dominated by dense clumps of bamboo, *Bambusa arundinacea*, which grow up to 25m. in height. There are two associations of bamboo in this forest: a)Areas closer to the deciduous forest have species such as *Schleichera oleosa* and *Xylia xylocarpa* which grow in moist deciduous forests, b) Areas closer to evergreen forest have evergreen species, notably *Cinnamomum macrocarpum*, which grows as a small tree in the evergreen forests. The undergrowth is mostly *Glycosmis arborea*, but sparse. Due to these associations, butterflies from the deciduous as well as the evergreen forests were seen in the bamboo forest.

6.Mixed deciduous forest: on the slopes towards the plains is the mixed deciduous forest which has a gradient of moist to dry deciduous tree species, reflecting the gradual decrease in rainfall. The trees may grow up to 25m., but average height of taller trees is about 20m. The undergrowth is not too dense or thorny, indicating that the forest is not much disturbed. Grasses are present, but not tall, and herbs are abundant. The dominant tree species are *Albizia odoratissima, Terminalia* spp., *Schleichera oleosa,* and *Cassia fistula.*

7.High-elevation evergreen (Shola) forest: this forest grows above 1,800 m. and only in the valleys. It is present in Tamil Nadu side of Anamalais only at the Grass Hills World Heritage Site. The trees are stunted, branches gnarled, and do not grow above 15m. *Rhododendron nilagiricum, Elaeocarpus recurvatus, Ilex* spp., *Syzygium* spp. are characteristic trees. All the dead wood is covered with dense mats of mosses. The undergrowth is dense, dominated by acanthaceous shrubs which makes a thick web of branches. Thorny canes (*Calamus* spp.) are very common, making the forest impenetrable. March and April are the only dry months, precipitation in other months in form of rain or dew is considerable. Along with shola forest, higher mid-elevation forest at 1,500m., which is structurally similar, was sampled and pooled with sholas.

8.Mid-elevation evergreen forest: the evergreen forest at Varagaliar was chosen as the sampling site for this vegetation type. It is situated in a long valley that is between half and a kilometre wide. The forest is tall, up to 40m., with emergents even taller. Dipterocarps, especially *Vateria indica, Hopea parvifolia* and *Dipterocarpus indicus*, are most common among large trees. Canopy is closed but for some tree-fall gaps. Vegetation is dense in all the horizontal layers, but nowhere impenetrable since the forest is not disturbed. The undergrowth is composed of tree saplings, shrubs, tall acanthaceous herbs and a species of grass, *Oplismenus compositus*, which grows only under shade of the moist forests. Towards ridge-tops this forest gives way to drier and stunted vegetation.

2.3.Methods For Vegetation Sampling: Since it was my first experience of vegetation sampling in the evergreen forests and savannah where almost all the plants were new to me, I did not sample vegetation for plant species diversity. Instead, I used data (Utkarsh 1998) from the Western Ghats Biodiversity Network (Gadgil 1996a, 1996b), which was already available. For calculating foliage height diversity, I enumerated plots of 20X10m. in the evergreen forest, deciduous forest and teak plantation, and 1X1m. in the savannah and high-elevation grassland. I enumerated in the plots all the plants that were equal to or greater than 1 cm. GBH, recorded the height at which their foliage began, where it ended, and spread of foliage. Based on these three, I calculated amount of foliage in each horizontal vegetation layer. To facilitate comparison with other studies I made following vegetation layer categories: 1) Evergreen forest- a)herb layer (0-1 m.), b)shrub layer (1-10m.) c)small tree layer (10-25 m.), d)large tree layer (>25 m.). 2) Deciduous forest- a)herb layer (0-1 m.), b)shrub layer (1-3m.) c)small tree layer (3-10 m.), d)large tree layer (10-20 m.). Heights of the vegetation layers in evergreen and deciduous forests are different because the forests are of different heights, and accordingly height of different growth forms vary in these two vegetation types. I calculated foliage height diversity using Shannon's diversity index (Magurran 1988).

2.4.Butterfly Sampling:

2.4.i. Butterfly species diversity: a. ground sampling: In each of the vegetation types I chose an area that was away from abrupt edges and ecotones leading to other vegetation types. I avoided places with known or apparent impact of major disturbances in the past. Based on earlier experience and initial surveys of the study area, the areas chosen were taken to represent the vegetation types with fairly consistent vegetation structure. In these selected patches I took butterfly counts from November 1998 through February 1999. Then the butterfly populations in very open vegetation types, namely, high-elevation grassland, shrub savannah and teak plantation, reached their trough, so I abandoned sampling. During the summer months I saw hardly 2 or 3 butterflies in these dry vegetation types after walking double the distance than the usual distance covered for earlier counts.

The usual distance covered during an individual count was my 900 steps, which amounts to about 600m. When I did not encounter 40 butterflies in the 900 steps, I continued along the line until I got 40 individuals, and this was recorded separately. Thus, my basic data consist of butterfly counts in 600m., reinforced by additional individuals for use in rarefaction analysis which was the main statistical tool I used for calculating butterfly species diversity. I took the counts by walking in one direction, but not necessarily a straight line by magnetic compass. Different places in a vegetation type in the same area were chosen for butterfly counts in different months. I recorded all butterflies seen during the counts, with their horizontal distances from the count line, and the heights at which they were seen first, as well as the date, time of the day and general weather conditions during the count. The counts were taken between 9.00a.m. and 3.30p.m. Although visibility in different vegetation types and for different size classes of butterflies is liable to be different, I did not fix land width during the counts. All the butterflies thus seen were included in the analyses. This methodology is similar in general characteristics to others used for earlier studies on butterflies in India (Kunte 1997, Kunte *et al.* 1999). This is because my effort was directed towards estimating butterfly species diversity, and not the density. However, frequency of butterfly sighting per hundred steps may act as a surrogate for density. For calculating species diversity it is essential to record merely number of individuals of the species seen. Density is a useful parameter in many studies, but since the main thrust in this study was on rarefaction analysis and species richness, inclusion of all the individuals in the analyses with disregard to density was effective. The rarefaction analysis automatically corrects for effects of sample size and number of individuals in each sampling unit (Ludwig and Reynolds 1988).

b. Canopy sampling: For recording layer use by butterflies, I sampled butterflies in the canopy and middle layers with help of climbing equipment. The climbing equipment- ropes, jumars, descender, harness, karabiners, etc. is standard equipment used for rock climbing and abseiling (rappelling). A pilot rope fixed over a branch of an emergent/canopy tree pulled the climbing rope over the branch, which I used to climb on the tree. I took observations in three layers- the ground (0-10m.), middle layers (10-25m.), and the canopy (>25m., usually up to 40m.). Visibility in all the layers was about 15-20m. Since mine was the first attempt of arboreal sampling of butterflies in India, I restricted the records to mere presence or absence of species from the layers. However, their numbers were noted during quantitative sampling. Height from the ground, distance from the count point, etc. were not recorded because humans being terrestrial animals, judgement of precise height and distance invariably goes wrong while sampling from the canopy for the first time. Only a long-term study and practice would cure this problem.

I sampled canopy only in the evergreen forest because only in the evergreen and semi-evergreen forests even the tiniest butterflies go to canopies (data of Kunte *et al.* 1999). In the mixed deciduous forests such as the one sampled during this study, I observed mostly large butterflies (e.g. Great Orange-tip, Crows, Southern Birdwing; only few small species- e.g. Pea Blue and Royals; for scientific names of all butterfly species mentioned in the thesis, see a note under Appendix 1) were observed flying at the tree-tops. Secondly, it was possible to see and identify from the ground butterflies in the crowns of trees in the deciduous forests, I did not spend time in the deciduous canopies. On the other hand, sampling in the evergreen forest canopies was very useful because very small species such as the Lineblues and skippers were also present there, which could not even be seen from the ground.

I identified the butterflies with the aid of Evans (1932), Wynter-Blyth (1957) and my notes that I had prepared after examining butterfly specimens from the Bombay Natural History Society's insect collection.

2.4.ii. Body Measurements: I caught the butterflies and took their body measurements throughout the study period, but intensified this activity during February through May 1999. I netted the butterflies to record following measurements:

1.body length: from base of the labial palps to tip of the abdomen, 2.thorax length, 3.thorax width, 4.wingspan: from base of a wing to the tip, multiplied by two, and 5.proboscis length.

I took these measurements using a non-digital vernier caliper and a needle. The butterflies were held either by the thorax or base of the wings, depending upon which body parameter was being recorded. To measure proboscis length, the butterflies were held against the scale of the vernier caliper and the proboscis was straightened using a needle. After taking the body measurements, I released the butterflies.

2.5.Adult Feeding Plants, Larval Host Plants, and Resource Utilisation: Larval host plant data were mostly compilation from last about 120 years' published work. They were gathered from three major sources: 1.Bell (1910 to 1927), 2.Sevastopulo (1973), and 3.Wynter-Blyth (1957). I added up the compiled information by my personal observations, then cleared the data of synonyms and incorrect observations, and replaced old scientific names by current scientific names with the help of regional floras published after 1993 (mostly by Botanical Survey of India). I arranged the plants alphabetically, assigned them to families, vegetation types and growth forms using these floras, personal communications and my observations on these plants. I could not use Anamalais-specific regional information on larval host-plant utilisation because of its unavailability, but used the information that was published for butterflies from nearby regions, or for the Western Ghats as a whole. This may not affect the analysis, since out of 331 butterfly species so far recorded from the Western Ghats, about

90%, and 100% for which larval host plants are recorded, are found in the Anamalais (Evans 1910, Ugarte and Rodericks 1960). Close to 100% of the plant species or their close kin recorded as the larval host plants are found in this region (Fischer 1921). It turns out that out of 139 plant families, 764 genera and 1775 species found in the Anamalais (Fischer 1921), the butterflies use 83 families, 309 genera and 433 species. The numbers of plant taxa in Anamalais given by Fischer should be considered slightly less than the actual ones because there have been additions after his flora was written. Also, some families were split and new ones formed (e.g. *Bombax* and *Ceiba* were separated from Malvaceae, and put under a new family: Bombacaceae). However, the pattern of growth form and plant species richness across vegetation types may still be similar because the numbers of families, genera and species used for present analysis are probably too high to be affected by such relatively smaller changes. However, a more site-specific analysis of larval host plants may be needed in future.

I quantified adult food resources during the field work. There is very little information published earlier on this subject (e.g. Shahabuddin 1997), so most of data set used in this thesis was original. During the usual butterfly counts as well as all-out-walks (opportunistic sampling), I noted every new observation of a butterfly feeding on a flower. Along with it, I recorded following parameters: 1.butterfly species, 2.plant species, 3.corolla tube length, 4.flower size, 5.flower colour, 6.height from the ground at which the flower was placed, 7.growth form of the plant, 8.habitat, 9.solitory or inflorescenced flowers, 10.isolated flower(s) versus massive floral displays, 11.other flowering plants and non-visiting butterflies, if any, in the neighbourhood of the flowering plant on which the observation was made. I measured the floral parameters using a vernier caliper.

I compiled from available literature, and collected from the field, information on plant as well as non-plant resources of butterflies. However, for the present analysis I have included only plant resources that serve as larval and adult resources, because in larval stages the butterflies feed on only leaves, flowers or fruits of various plant species. The only south Indian exception to this is the Apefly (*Spalgis epius*, family Lycaenidae, subfamily Miletinae), whose caterpillars feed on mealy bugs (family Coccidae, an insect group). Among adult butterfly resources there are numerous exceptions, such as butterflies feeding at wet soil patches, bird droppings, rotting crabs, plant sap, mammalian sweat, etc. However, these resources are distributed more or less in all vegetation types and are not as diverse in their structure or placement as are floral resources. Therefore they may not form major structural entities in the vegetation types that can affect resource use by butterflies, by selectively restricting access to certain species. Hence, only plant resources seemed useful for such an analysis.

From the ground as well as canopy sampling data, plus observations during all-out-walks, I noted at which height the butterflies were seen. Based on these observations, I assigned the butterfly species that I saw in Anamalais to three horizontal vegetation layers: 1.herb-shrub layer, 2.small tree layer, and 3.large tree layer. I have classified butterfly plant resources into four growth form categories (herb and shrub layers making separate categories), but butterflies into only three layer use categories. This is because it was impossible to distinguish between herb and shrub layers as far as butterfly habitat use was concerned. All butterfly species that were restricted to ground vegetation layers moved in herb layer, and at least lower portion of shrub layer, so that both the layers shared all the butterfly species found in them.

All the data gathered or lists prepared for this thesis are available with me, and can be accessed free of any charge by anyone who has a research idea for which these data sets may be useful.

3. RESULTS :

3.1. Foliage Height Diversity and Plant Species Diversity: The foliage height diversity, as measured using Shannon's diversity index, increased from the high-altitude grassland to the evergreen forest, through intermediate shrub savannah, teak plantation and deciduous forest. The plant species diversity also increased in the similar fashion (Utkarsh 1998), which was the pattern also at the scale as large as the entire Western Ghats.

3.2.Butterfly Species Diversity: Table 1 gives the vegetation type-wise details; namely, number of counts in each vegetation type, total number of steps walked to finish these counts, number of individuals seen, and the frequency of butterfly sightings per hundred steps. There was no clear pattern across the vegetation types- butterfly frequency was neither correlated with the vegetation structure nor with the butterfly diversity in the vegetation types.

Results of rarefaction analysis are given in table 2, fig. 1, 2 and 3. Butterfly diversity increased from high-elevation grassland through shrub savannah, teak plantation, evergreen forest and deciduous forest. Vegetation type-wise butterfly species lists are in appendix 1, which give total species richness in the vegetation types. I saw about 180 butterfly species during the six months of the study, which are slightly over 80% of the field-identifiable butterfly species from Anamalais. Butterfly species richness also yielded the same pattern as above and is included in table 2 and fig. 4. Table 2 also gives diversity values derived using most commonly employed diversity indices, which would facilitate comparison of these results with others. All showed that butterfly diversity increased in the following vegetation type order: high-altitude grassland, shrub savannah, teak plantation, evergreen forest and deciduous forest.

Rarified butterfly diversity values for three horizontal vegetation layers in the evergreen forest, namely, 0-10m., 10-25m. and >25m., were close to each other, and not significantly different (Single-classification ANOVA, df=2, F=0.435, p=0.65). This is illustrated in fig. 3, and shows that there was only minor difference in butterfly diversity across vegetation layers.

3.3.Correlation Between Foliage Height Diversity, Plant Species Diversity and Butterfly Species Diversity: Figure 1 shows the correlation between butterfly species diversity (as calculated by rarefaction) and foliage height diversity. Although the correlation was significant (Spearman's rank correlation, n=27, r_s=0.451, p<0.05), the scatter was wide because intra-site, inter-count variation was considerable. Figure 2 shows the same correlation, but with all butterfly counts from each vegetation type pooled, which eliminated effect of the inter-count variation. This correlation (Spearman's rank correlation, n=5, r_s=0.828, p<0.05) also gave the same pattern as in fig. 1. Figure 4 shows correlation between butterfly species richness (as the total species richness from the vegetation type) and foliage height diversity. This correlation was stronger and more significant (Spearman's rank correlation, n=5, r_s=0.943, p<0.01) than the previous two. However, there was a serious problem in all these correlations. Although all the correlations were significant, the increase in butterfly species diversity was not linear with the increase in foliage height diversity. It increased from high-elevation grassland through shrub savannah, teak plantation and deciduous forest, then dipped down in the evergreen forest. However, the difference in values was not enough to turn the correlation insignificant. So the actual pattern was that until the vegetation types were more or less dry the butterfly species diversity increased linearly, and lowered in the evergreen forest. Both plant species diversity and foliage height diversity, on the other hand, increased linearly as the vegetation grew more complex in structure. James and Wamer (1982) illustrated such insensitivity of correlation coefficient to non-linear relationships, which hid an important diversity pattern in birds.

3.5.Layer Use by Butterflies: Details of layer use by each species seen during the present study are given in appendix 1. Out of 108 species from the evergreen forest, 39 species were seen in all the layers (between 0 and >25m.), 38 species in two layers (between 0 and 25m.), and 31 species in only one layer (between 0 and 10m.). Out of 117 species from the deciduous forest, 29 species were seen in all the layers (between 0 and 20m.), 37 species in two layers (between 0 and 10m.), and 51 species in only one layer (between 0 and 3m.). In the study site, only two vegetation types, namely, deciduous and evergreen forests had truly multi-storeyed vegetation structures. The layers had different heights in deciduous and evergreen forests because the forests themselves had very different heights. However, the layers roughly represent herb, shrub, small and large tree layers. The teak plantation also had tall trees, but it being a maintained plantation, the vegetation was not continuous between the shrub layer and the crown of the trees. Moreover, there were few resources in the crown, so less number of butterflies.

There were butterflies restricted to a single layer, but all such cases were the butterflies restricted to only herb and shrub layer, no species confined to only small tree or large tree layers. All the species seen among the tree layers were also seen in the herb and shrub layers. There was one exception, the Common Onyx, which was seen only once in only the small tree layer in the evergreen forest. However, it certainly frequents the herb and shrub layer (Wynter-Blyth 1957). Thus, the herb and shrub layer supported all the species, either because it had larval host plants or adult feeding resources of all the butterflies. However, there were drastic differences in abundance of butterflies between herb-shrub layer and large tree layer. While species such as the Clipper and Redspot Duke were as common in both the layers, some species, e.g. the Rustic and Common Sailor, were more common near the ground than among the tall tree crowns. On the other hand, although some of the large and more powerfully flying species, e.g. the Tailed Jay and Common Bluebottle, were found feeding near the ground, they were far more abundant in the canopy.

3.6.Resource Richness:

3.6.a.Larval host plants: Table 4 gives vegetation-type-wise and growth-form-wise breakup of larval host plants of the butterflies. When host plants of all the growth forms were considered, high-elevation grassland had lowest richness, followed by shrub savannah, scrub and deciduous forest. Evergreen forest had second-highest richness of larval host plants. The resource distribution in horizontal vegetation layers in the evergreen and deciduous forests was uneven. There were more larval host plants as shrubs and small trees, than herbs and large trees, than expected if the resources were evenly distributed (Chi-square test for goodness of fit, $X^2_{0.001[3]}=22.776$ and 20.14, respectively, for two forest types).

3.6.b.Adult feeding plants: Table 5 gives vegetation-type-wise and growth-form-wise breakup of adult feeding plants of the butterflies. Similar to larval host plants, resource richness increased from high-elevation grasslands to deciduous forest, but that in the evergreen forest was even slightly higher. However, the differences between scrub and teak plantation, and between evergreen and deciduous forests, were too small. Differences in growth forms used, however, were drastic. The butterflies used mostly herbs and shrubs as feeding plants, than small and large trees, than expected if all the growth forms were equally used (Chi-square test for goodness of fit, $X^2_{0.005[3]}=13.89$ for the deciduous forest and $X^2_{0.025[3]}=10.09$ for the evergreen forest).

3.6.c.Total resource richness: When larval host plants and adult feeding plants were pooled to get total plant resource richness for the butterflies, pattern of resource richness remained the same as for the larval host plants (table 6). The deciduous forest was most resource rich, followed, in the decreasing order, by the evergreen forest, scrub, shrub savannah and high-elevation grassland. Overall, in the evergreen forest the butterflies used small trees much more than the large trees and herbs (Chi-square test for goodness of fit, $X^2_{0.001[3]}=21.72$). In the deciduous forest, resources were relatively equally distributed across growth forms, but the large trees were still much less used (Chi-square test for goodness of fit, $X^2_{0.01[3]}=12.48$).

Fig. 5 shows a significant, positive correlation between vegetation complexity and resource richness (Spearman's rank correlation, $n=5$, $r_s=0.9$, $p<0.05$). However, when total plant resource richness was plotted against butterfly species richness for the vegetation types (fig. 6), the correlation was much more strong, significant and positive ($n=5$, $r_s=1$, $p<0.0001$).

<u>3.7.Adult Butterfly Resource Use:</u> As mentioned in section 3.6.b, most of the adult feeding plants were from the herb-shrub layer. To analyse floral parameters and consequent resource use by butterflies, I used corolla tube lengths. Corolla tube length appeared most effective in isolating butterflies from each other in terms of resource use. Fig. 7 shows a scatter-plot with 193 points of corolla tube lengths of flowers that the butterflies used and proboscis lengths of the butterflies that used these flowers. These 193 points belonged to 71 plant species and 76 butterfly species. The correlation was positive and significant (Pearson product-moment correlation, $n=193$, $r=0.628$, $p<0.001$). However, apart from the expected pattern of resource use, namely, that the butterflies with longer proboscis lengths would feed on flowers with longer corolla tube lengths, there are many points representing butterflies that fed on smaller flowers despite having much longer proboscis. It is obvious that a butterfly can reach nectar from all the flowers that have corolla tubes equal or shorter in length than its proboscis. However, the surprising points are those representing butterflies with shorter proboscis that fed on flowers with relatively longer corolla tubes. Although such points were few compared to total observed points, they are worthy of special attention because they tend to diffuse or even contradict logically expected pattern of resource utilisation by butterflies.

4. DISCUSSION :

One of the important results of this study was that the butterfly species diversity was not linearly correlated with foliage height diversity. This pattern has also been described in small mammals and birds (August 1983, Daniel *et al.* 1992, Tomoff 1974, Willson 1974). MacArthur and MacArthur (1961) pointed out that plant diversity was positively correlated, and contributed, to foliage height diversity. Although I did not measure plant species diversity in Anamalais, this pattern holds true also on the scale of entire Western Ghats (Utkarsh 1998). However, MacArthur showed positive linear correlation between foliage height diversity and bird species diversity, whereas butterfly species diversity, in Anamalais, did not show this pattern. This pattern persists also on a much larger scale of the entire Western Ghats (Kunte *et al.* 1999). It is clear from this and other exceptions pointed out by MacArthur and ecologists following him that diversity in any animal group may or may not be positively correlated with either foliage height diversity or plant species diversity (August 1983, Daniel 1992, James and Wamer 1982, Karr and Roth 1971, MacArthur *et al.* 1962, Murdoch *et al.* 1972, Pearson 1971, Tomoff 1974, Willson 1974). In Anamalais, butterfly diversity gradually increased from the grassland to the deciduous forest, but lowered in the evergreen forest. This means it followed the pattern of increasing foliage height diversity, as predicted by MacArthur and MacArthur (1961), only in the relatively dry vegetation types. Although there is considerable endemism, evergreen forests of the Western Ghats are relatively poor in bird (Daniel *et. al.* 1992) and butterfly (Gaonkar 1996) diversity due to historical reasons. Since the peninsular Indian climate gradually became dry in geographical time scale, extent of evergreen forest in this region contracted, deciduous forests extended, and the evergreen forests of the Western Ghats became isolated. This did not happen in NE Indian and SE Asian evergreen forests, which are contiguous. Probably this is the reason the Western Ghats evergreen forests are depauperate in bird species richness as compared with richness in the deciduous forests

(Daniel *et al.* 1992), and it applies to butterflies as well. A glance at butterfly fauna suggests that the evergreen forests in the NE India, on the other hand, seem to be more species rich than the deciduous forests. There, the foliage height diversity and butterfly species diversity may be linearly correlated. But it should be noted that during and after publishing his 1961 paper, MacArthur himself had faced some exceptions to the pattern his theory predicted (MacArthur 1964, 1965). Later studies had produced mixed results; some supporting the theory, others contradicting it, and yet others showing vague patterns. This indicates that there may be something else, rather than foliage height diversity, responsible to species diversity (Karr and Roth 1971).

It is intuitive that animals that are host-plant-specific would exhibit maximum diversity where plant diversity is highest. Since foliage height diversity and plant diversity are correlated, it is intuitive to expect linear correlation between also foliage height diversity and such an insect group. This brings forth a question: why would diversity of an insect group that is exclusively dependent on plants vary independently of plant and foliage height diversity? To discuss this, I will first spell out the underlying assumptions in MacArthur's theory, treat them with help of patterns revealed during this study on butterflies, and try to explain why butterflies did not show the pattern assumed and/or predicted by foliage height diversity theory. This in turn may help explain why this theory does not satisfactorily explain diversity pattern in all habitats and at all sites.

Although MacArthur and MacArthur (1961) did not explicitly mention assumptions in the evolutionary mechanism proposed, there were four major assumptions: i)resources for a species are evenly dispersed within a horizontal vegetation layer. Therefore a species can travel in the layer without wasting time or energy because "between any two fairly distant feeding places there will be a fairly natural route also consisting of feeding places." (p.597). ii)resources are unevenly dispersed across the horizontal layers. Therefore it will be costly for an animal to ~~travel~~ across layers, forcing it to restrict to a single layer. iii)even for generalist species, the cost of switching over between layers is high, which would preclude switching over between layers. The generalist species would tend to diffuse or eliminate the pattern identified by MacArthur and MacArthur (1961), that each additional horizontal layer of vegetation had the same number of species, independent of which layers were already present. iv) If the first three assumptions are true, the species would more or less adapt to utilising resources within a horizontal layer and restrict themselves to particular layers that most suit them. Therefore each horizontal layer of the vegetation would have a different set of species. Thus, each layer would add similar magnitude of diversity in more complex habitats.

I did not quantify spatial resource dispersion, so am not able to demonstrate that resources are or are not distributed homogeneously within a layer. However, it could be possible that resources are randomly and unpredictably dispersed within a layer. In such a case, there need not be any continuous passage within a layer with feeding resources all along in an individual's movement path.

The second assumption is certainly not true. Butterflies, and so do the birds, travel through more than one layer in a short span of time, and also feed along the way. The Southern Rustic, for example, was observed feeding on flowers of *Ageratum, Lantana, Antidesma menasu, Premna*, and a liana; each representing a vegetation layer at a different height. Similarly, the Common Albatross fed on flowers of *Ageratum, Leea, Vernonia arborea, Cinnamomum wightii* and a large liana, again each plant representing a different vegetation layer or growth form. Among birds, the flycatchers and bulbuls are often observed travelling between bushes and tree crowns in the tall evergreen forests, hunting insects and picking fruits at whichever place they are available. As for within vegetation layer dispersion, I did not quantify spatial dispersion of resources across vegetation layers, too. However, the fact that the butterflies travel and feed in different vegetation layers during their peak feeding activity time itself is evidence that resources are available across the layers. This also suggests that switching over between layers is not costly in time or energy. The switching over between horizontal layers will be adaptable if there are considerable benefits of doing so after canceling its cost. The cost will be offset and additional benefits acquired if the probability of finding utilisable resources across layers is high. Moreover, if: i) the resources are clumped in all layers (such as plants with flowers in inflorescence, or with massive floral display), and ii) probability of finding a resource random, but benefits of finding a clumped resource very high, then rewards of switching-over between the layers are higher than the cost. This seems to be a real-life situation, because most of the plants on whose flowers I found butterflies feeding, had either inflorescence (e.g. *Vernonia, Andrographis and Ixora*) and/or massive flower displays be the flowers solitary or not (e.g. *Vaccinium, Schleichera oleosa*). There is still another face of this problem in higher animals, especially higher vertebrates, such as birds and mammals. These animals learn and memorise sources of food and repeatedly visit those sources. Thus, after a frugivorous bird learns about a particular fruiting tree and its fruiting season, it visits that tree in the right season. Among insectivorous birds, certain species that participate in the mixed hunting parties are attracted towards vocalisation of other species that participate in the mixed hunting parties and thus track the resource without spending much energy and time; in fact they save time. For a generalist species that has feeding acceptance to more variety of food items, it is even less costly to switch-over between layers. This would further obscure the pattern predicted by MacArthurs' theory. As a result, there would be small number of species restricted to a layer. This contradicts the fourth assumption.

Fig. 7 shows an interesting pattern of resource use by butterflies. As discussed earlier in section 3.7, there are many points representing butterflies feeding on smaller flowers despite having much longer proboscis. Naturally, a butterfly can take nectar from the flowers that have corolla tubes equal or shorter in length than its proboscis. Since in butterflies body length is positively correlated with proboscis length (fig. 8, Pearson product-moment correlation, n=295, r=0.628, p<0.001), as the size of the butterfly increases, it is increasingly at an advantage because it would encounter more and more flowers of varied corolla tube lengths in the range from which it can take nectar. However, smaller flowers would generally have smaller quantities (absolute, not relative quantities) of nectar. The question, therefore, is of. energetics of flight, nectar-searching efficiency, and reward of nectar quantity from small versus large reservoirs of nectar. In other words, it is a choice between small versus large flowers relative to a butterfly's proboscis length and body size. Small flowers means visits to more number of flowers, more landings and take-offs, and smaller reward per flower or visit. On the other hand, large flowers means less number of visits, and higher gains per visit to a flower. Landing and take-offs themselves may not be very costly, but the time spent on smaller flowers, rather than on the larger flowers, may be a big cost. However, since the butterflies seem to be not so rigid about choosing flowers in terms of the flower size relative to their body size (fig.7), this energetic "constraint" seems to be less effective. Considering the range of corolla tube lengths that a butterfly would encounter (see fig.7), it seems obvious that butterflies medium to large in size would have access to a large number of flowers, making the resources suitable for their utilisation virtually omnipresent. Therefore at least for medium to large butterflies there seems to be little cost involved in switching over between layers. Even some short-proboscis butterflies fed from flowers with relatively longer corolla tubes, which is also reported in bees (Belavadi *et al.* 1997). If this pattern is as much, or more, prevalent on a wider scale, then probably even the 'relatively-longer-corolla-tubes' constraint may not seriously affect accessibility to the butterflies of the nectar. Therefore resources for smaller butterflies, too, would be omnipresent, in all the layers, which would reduce the cost of time and energy in switching over between layers predicted by MacArthur. Thus, both the factors discussed in this paragraph disagree with first two assumptions.

In connection with the previous paragraph, fig. 8 reveals that body length increased slightly more rapidly compared to proboscis length. Butterflies could have developed varying body sizes for phylogenetic and ecological reasons, but their proboscis have remained in a less wide range. Perhaps it was adaptive for butterflies or nectarivores in general, to save on producing long proboscis. From fig.7 it appears that butterflies mostly use flowers with short corolla tubes, although many of them could also use longer ones. It could be just that most of the plants that offer nectar to butterflies have short corolla tubes. Without going into details of that, it can be said that when most of the plants offering nectar bait have short corolla tubes, butterflies have access to more species of flowers than they would have if corolla tube range was greater.

Data on butterfly resource richness across vegetation types suggest that there need not be a linear correlation between foliage height diversity, resource richness and plant species diversity (table 6 and fig.5). Although butterflies are directly dependent on plants in larval and adult stages, they do not use all the plant resources equally. Plus, not all plants are used as resources. If plants from only a few vegetation types are used more, or some plants from a vegetation type are used much more than other plants from the same vegetation type, then the pattern of butterfly species diversity may depart from that of the patterns of plant species diversity and foliage height diversity. This seems to be the case with butterflies in the Anamalais.

Foliage height diversity or heterogeneity indices correlate well with animal diversity in many cases, although not all. However, Willson (1974) cautioned use of indices in ecological studies and urged to understand properties and relevance of these indices in ecological studies. On the other hand, Karr and Roth (1971) suggested that the scatter in a foliage height diversity and bird species diversity relationship involving temperate and tropical habitats could be a result of important but unmeasured variables which affect bird species diversity. Foliage height diversity or other habitat parameters are most probably not direct determinants of species diversity but only correlates or clues of other parameters that the animals use (1985). Considering these three opinions, and a fact that all earlier explanations of habitat parameters and species diversity correlations lingered at resource dispersion and richness that were almost never completely measured, it now seems appropriate to concentrate on resources. However, probably a direct approach is needed. For this purpose, it may be necessary to understand which birds (or other animals) feed on which insects (or resources), not merely that a bird is an insectivore. For phytophagous insects, it would be necessary to find out which plants are utilised as resources, and how are these resources dispersed across and within vegetation types.

In this connection I propose a hypothesis, which I call "sociable host hypothesis" for butterflies (fig. 9 and 10). I define a "sociable host" as a plant that supports many butterfly species in their larval stages- the plant is sociable, it "likes" its insect associates. Thus, high sociability means a plant supports many butterflies and low sociability means a plant supports only one or few butterfly species. This hypothesis differs from theories that involve vegetation structure. In fact it suggests that resource dispersion and utilisability may primarily decide species diversity, and vegetation structure may be a frequent correlate of these two factors. Vegetation structure may only indirectly affect butterfly species diversity by varying resource dispersion. However, resource richness and dispersion may also be independent of vegetation structure. This theory considers vegetation types differently just because they offer differential diversity levels of plants, which may affect utilisable chemical diversity at disposal of the butterflies. Plant diversity increases from simple to complex vegetation types. If chemical diversity is relatively evenly dispersed across plant growth forms and families in different vegetation types, complex vegetation types will naturally have more chemical diversity because they have more species of plants (fig. 9). On the other hand, due to high herbivory pressure, plants in some complex vegetation types, e.g. evergreen forests, have high amount of secondary compounds, making themselves palatable only to very specialised herbivores. Thus, there are two opposing forces (fig. 10). Higher plant diversity in complex vegetation types can potentially offer higher diversity of resources, but their higher secondary compound diversity and content would tend to reduce sociability. However, butterflies do not use in their larval stages all plant families and species. Since occurrence of butterfly species is strongly influenced by larval resource distribution (Ehrlich 1984), only those species that are used by caterpillars would be considered as resources when discussing chemical diversity and sociability. From earlier work on larval resource use of south Indian butterflies (Bell 1910-1927, Sevastopulo 1973 and Wynter-Blyth 1957) it is seen that different plants support different diversity levels of butterflies; all resources are not equal. Some resources may be less or more varied in chemical composition and structure, are suitable for exploitation in many ways by many species or demes of the same species, therefore may offer more opportunities for speciation. Thus, they would tend to be more sociable. There would be a continuum (fig. 9), however, that many plants would support only one or two butterfly species (low sociability), some will support unusually large number of butterfly species (high sociability), and some will be intermediate in their usefulness as a resource (moderate sociability). There are indications of this pattern in larval host plant data so far published (Bell 1910-1927, Sevastopulo 1973 and Wynter-Blyth 1957). Most of the plants are used by only one butterfly species each. Some plants are used by many butterflies, for example, *Capparis* spp. and *Cadaba fruticosa* (both family Capparaceae) are used by eight butterfly species. *Xylia xylocarpa* (family Mimosaceae) is on top in the list, it supports 15 butterfly species in their larval stages. In all, 22 species from Mimosaceae are used as larval host plants and together they are hosts to more than 30 butterfly species, which is 10% of the Western Ghats butterfly diversity. When plants such as *Xylia* are present, even a single plant species can support extraordinary number of butterflies. When several of such highly sociable plant species are present in a relatively plant species poor vegetation type, they can support higher butterfly diversity than a vegetation type with higher number of less sociable plant species. It is noteworthy that although the evergreen forest in the Anamalais had higher plant species diversity as well as foliage height diversity than the deciduous forest, the deciduous forest had higher butterfly species diversity. The relevance of this in the present context is that *Xylia* and *Capparis*, both are predominantly deciduous forest elements. Family Poaceae: the grasses and bamboos, supports another almost 60 butterfly species in the Western Ghats. Poaceae also is a family of predominantly deciduous members with only a few species in the evergreen forest.

The hypothesis that butterfly species diversity would be dependent more on chemical diversity and sociability of host plants, rather than vegetation structural parameters, needs further detailed analysis of larval host plants and their utilisation by different butterflies. This hypothesis in the present form can be applied to other phytophagous insects as well. However, it needs better theoretical framework, which is a challenge ecologists will have to face to explain diversity on earth.

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TABLE 1. DETAILS OF BUTTERFLY COUNTS

Vegetation type	No. of counts	No. of steps	No. of individuals	Frequency (no. of individuals/100 steps)
Evergreen forest	7	7,970	524	6.57
Deciduous forest	4	3,600	423	11.75
Teak plantation	4	5,570	203	3.64
Savannah	4	6,350	199	3.13
High alt. Grassland	4	25,000	176	0.7
Total	27	56,640 (ca.35.5 km.)	1,731	

TABLE 2. BUTTERFLY SPECIES DIVERSITY ACROSS VEGETATION TYPES

Diversity index	High-alt. Grassland	Shrub savannah	Teak plantation	Deciduous forest	Evergreen forest
Rarifaction (No. of spp./11 ind).*	2.5, 4.38, 5.49, 6.20	3, 4.61, 5.36, 10	5.46, 6.91, 5.42, 8.11	8.12, 6.99, 7.63, 7	7.96, 7.78, 6.60, 6.22, 7.75, 6.57, 5.56
(No. of spp./96 ind), pooled	15.53	18.69	21.3	29.46	27.38
Shannon H'	0.74	1.00	1.12	1.37	1.27
Alpha	6.22	6.91	9.26	16.44	15.11
Berger-Parker Dominance (1/d)	1.70	2.89	4.41	6.31	5.29
Simpson's Diversity (1/D)	2.78	6.47	8.62	15.19	10.27
species richness	11	24	73	117	108

*Rarified diversity value (no. of spp./11 ind.) is given for each count under the respective vegetation types. Since number of counts in the evergreen forest was seven, there are seven values under that vegetation type; for the rest, only four. For rest of the diversity indices, all the counts from each vegetation type were pooled, so each index has a single value for a vegetation type.

TABLE 3. LAYER USE BY BUTTERFLIES

	Herb and shrub layer	Small tree layer	Large tree layer	Only herb and shrub	Herb to small tree	Herb to large tree
Evergreen forest	107	77	39	31	38	39
Deciduous forest	117	66	29	53	37	29

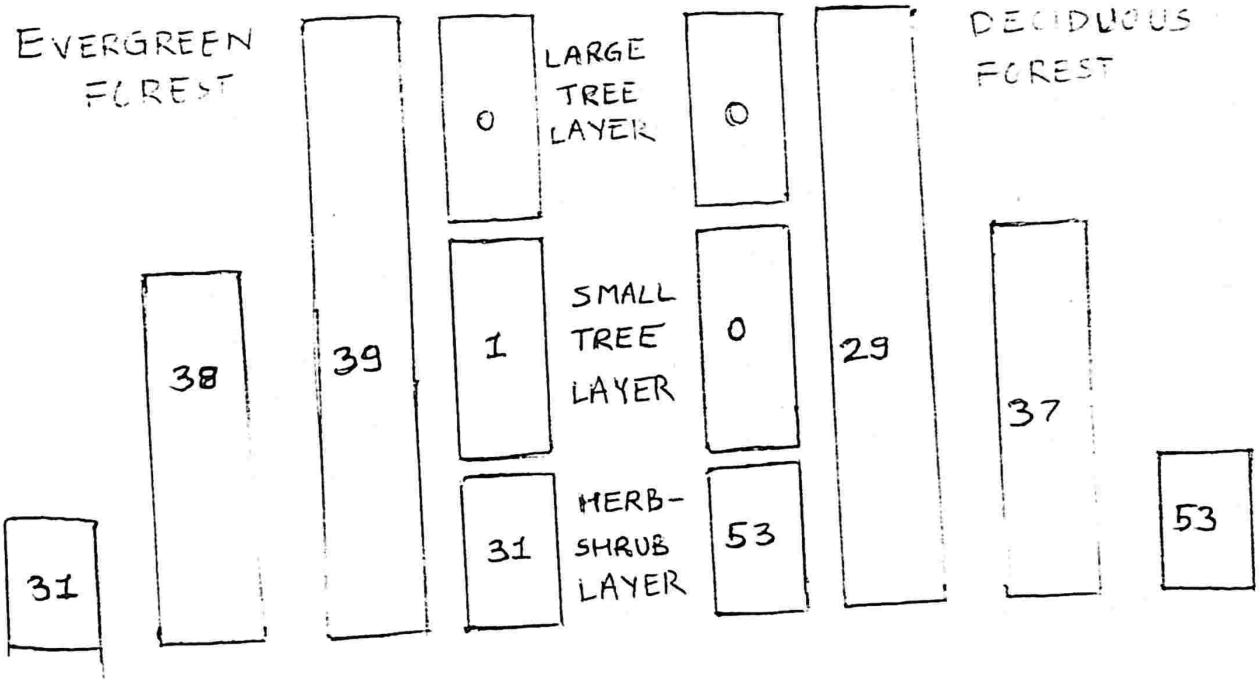


Table 3 gives butterfly species distribution across horizontal vegetation layers in the evergreen and deciduous forests. The first three columns give numbers of species that are found in the specified layer. The last three columns give numbers of species with a range indicated in the top row of vegetation layers used, without consideration of whether they are shared with other layers or not. Figure at the bottom of the table represents the same information, in a different form.

TABLE 4. LARVAL HOST PLANTS

	Herb	Shrub	Small tree	Large tree	Epiphyte/climber	Total
Evergreen	27	34	45	13	25	125
Deciduous	47	55	62	30	40	201
Scrub	34	28	15	1	12	74
Savannah	25	16	1	0	3	39
Grassland	27	11	0	0	0	37
Total*	71	81	85	38	59	

*Table 4 gives a vegetation type-wise and plant growth form-wise break-up of larval host plants of butterflies. Discrepancy observed between addition of the individual entries under respective growth forms and grand total written in the last column arises because growth forms of certain plant species are overlapping; for example, some plants are small to large trees or shrubs to small trees. These plants were entered under both the growth form categories. It is the case with grand total of growth forms across vegetation types also, where some plant species are shared between two or more vegetation types. The data are from Haribal (1992), Sevastopulo (1973), Wynter-Blyth (1957), and supplemented by personal observations as well as records supplied by Mr. E. Kunhikrishnan. Information on plants from scrub was available, so it was also included in this table, but from the teak plantations was unavailable. However, teak plantations being a man-made habitat in different soil, rainfall and temperature regimes, and varying maintenance treatments, is an amorphous vegetation type, with no plant species of its own, except the teak.

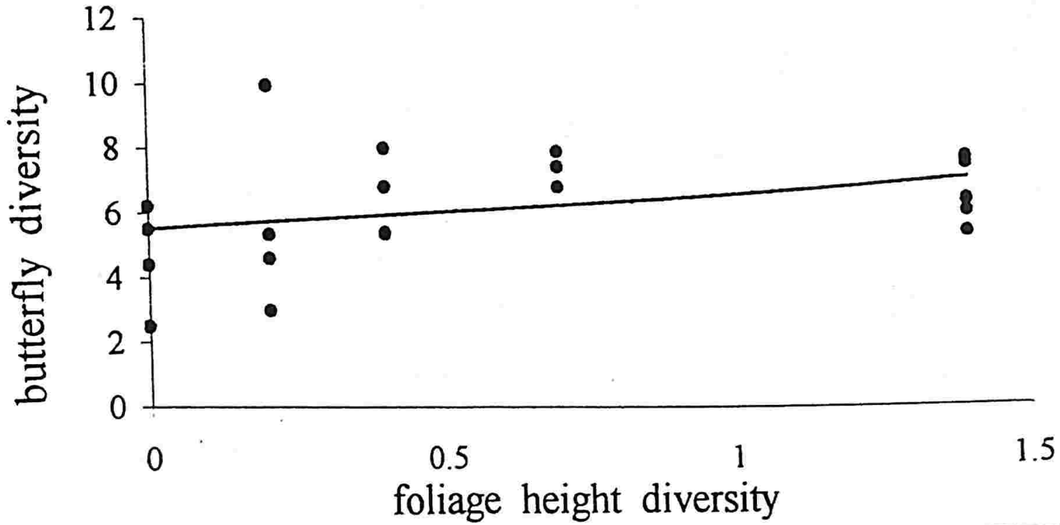
TABLE 5. ADULT FEEDING PLANTS						
	Herb	Shrub	Small tree	Large tree	Epiphyte/climber	Total
Evergreen	13	13	7	1	3	36
Deciduous	17	7	4	5	1	32
Teak	13	6	0	0	0	17
Scrub	13	3	1	1	0	18
Savannah	10	2	0	0	0	12
Grassland	7	0	1	0	0	8
Total*	31	14	9	6	3	

*see a note under table 4. This table presents only those plant resources whose flower nectar is utilised by adult butterflies. The data are from my field diaries of Nov. '98 through May '99, supplemented by notes from Mr. E. Kunhikrishnan, Dr. P. Pramod, and Mr. K. A. Subramanian.

TABLE 6. TOTAL PLANT RESOURCES						
	Herb	Shrub	Small tree	Large tree	Epiphyte/climber	Total
Evergreen	36	42	51	14	28	151
Deciduous	59	59	64	33	41	221
Scrub	43	28	15	1	11	82
Savannah	31	17	0	0	3	46
Grassland	31	11	1	0	0	42
Total*	96	88	91	41	61	

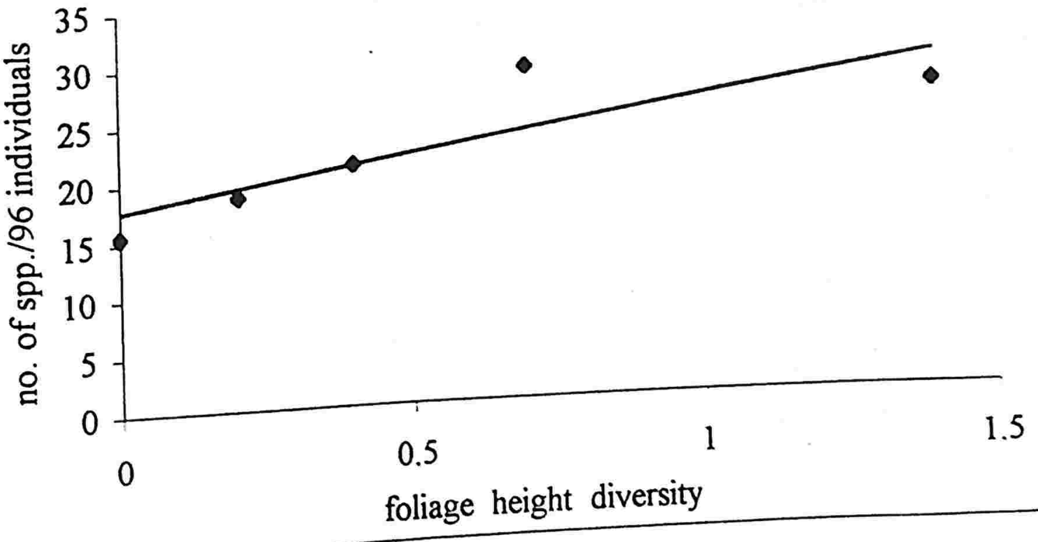
*see a note under table 4. In this table, larval and adult feeding resources are pooled (from tables 4 and 5), to get total plant resource richness across vegetation types.

FIG. 1. CORRELATION BETWEEN FOLIAGE HEIGHT DIVERSITY AND BUTTERFLY DIVERSITY (n=23, rs=0.458, p<0.05)



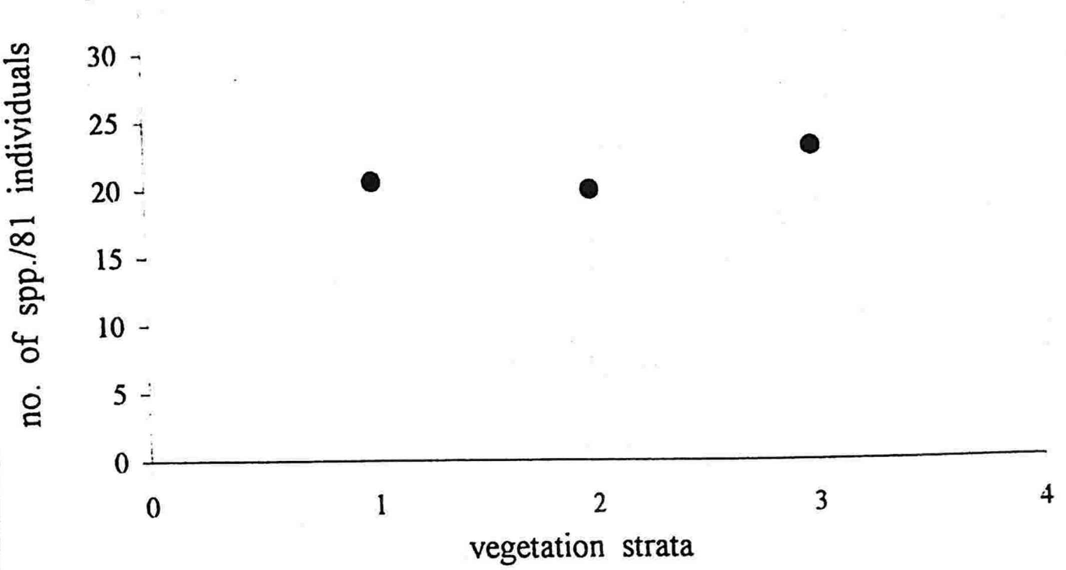
In fig. 1, the foliage height diversity points, from left to right, represent: 1)high-elevation grassland, 2)shrub savannah, 3)teak plantation, 4)deciduous forest, 5)evergreen forest.

FIG. 2. CORRELATION BETWEEN FOLIAGE HEIGHT DIVERSITY AND BUTTERFLY SPECIES DIVERSITY (n=5, rs=0.828, p<0.05)



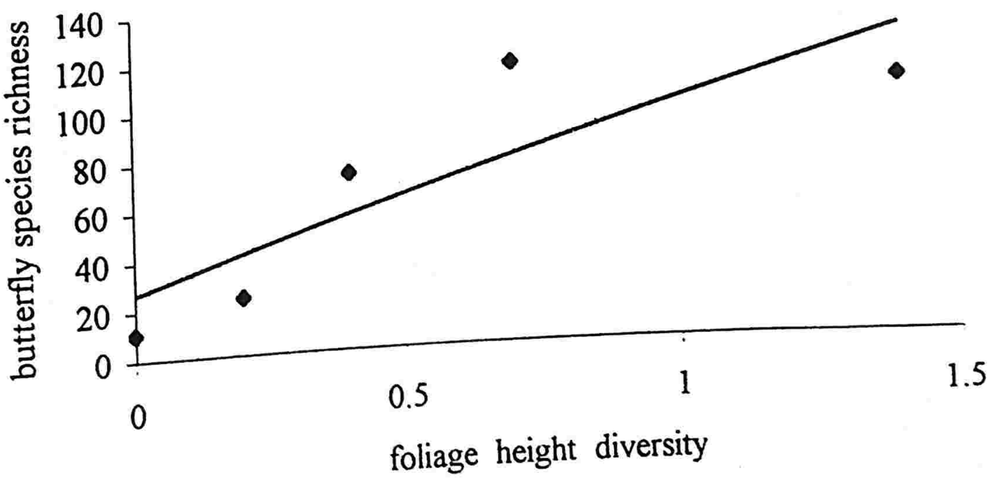
Foliage height diversity gradient same as in fig.1.

FIG. 3. BUTTERFLY SPECIES DIVERSITY ACROSS STRATA (df=2, F=0.435, p=0.645)



*points in fig.3 represent, from left to right, horizontal vegetation layers in the evergreen forest: 1)ground (herb and shrub) layers- (0-10m.), 2)middle (small tree) layer (10-25m.), 3)canopy (large tree) layer (>25m.).

FIG. 4. CORRELATION BETWEEN FOLIAGE HEIGHT DIVERSITY AND BUTTERFLY SPECIES RICHNESS (n=5, rs=0.945, p<0.05)



Foliage height diversity gradient same as in fig.1.

FIG. 5. CORRELATION BETWEEN VEGETATION COMPLEXITY AND RESOURCE RICHNESS (n=5, rs=0.9, p=0.05)

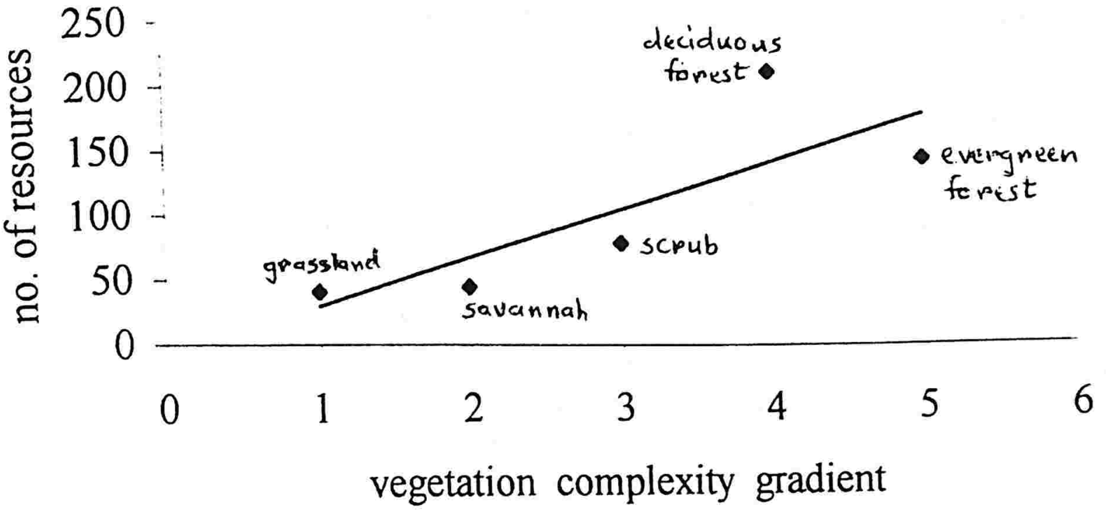


FIG. 6. CORRELATION BETWEEN RESOURCE AND BUTTERFLY SPECIES RICHNESS (n=5, rs=1, p<0.0001)

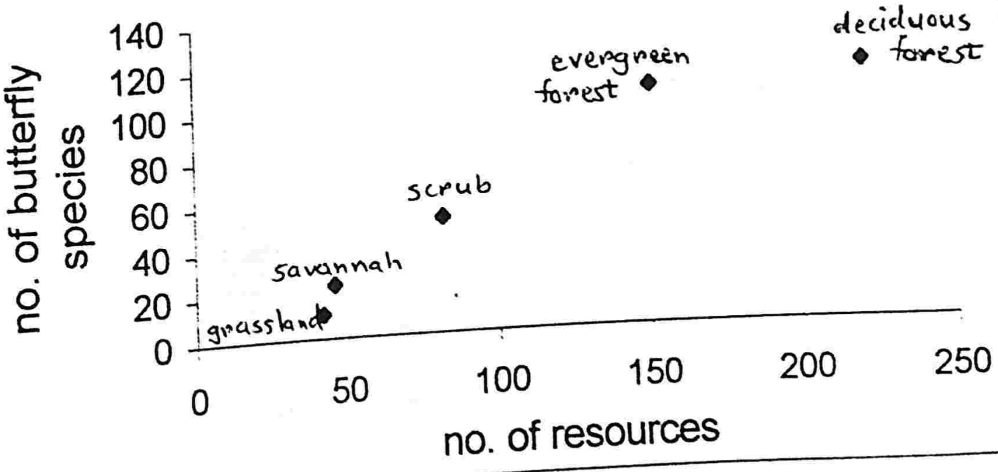


FIG. 7. CORRELATION BETWEEN PROBOSCIS AND COROLLA TUBE LENGTHS (n= 193, r= 0.628, p<0.001)

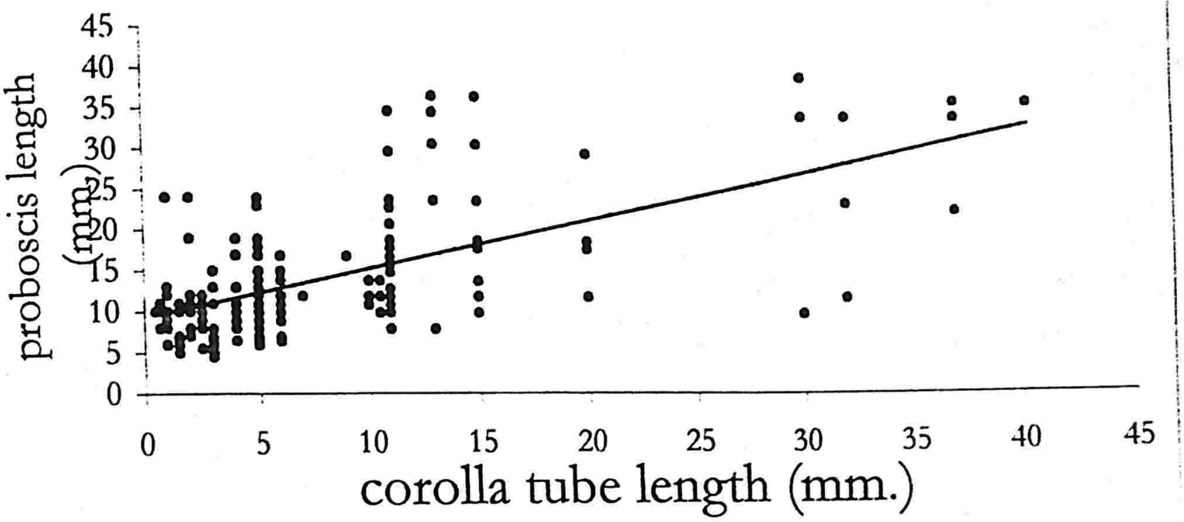


FIG. 8. CORRELATION BETWEEN BODY AND PROBOSCIS LENGTH (n=295, r=0.628, p<0.001)

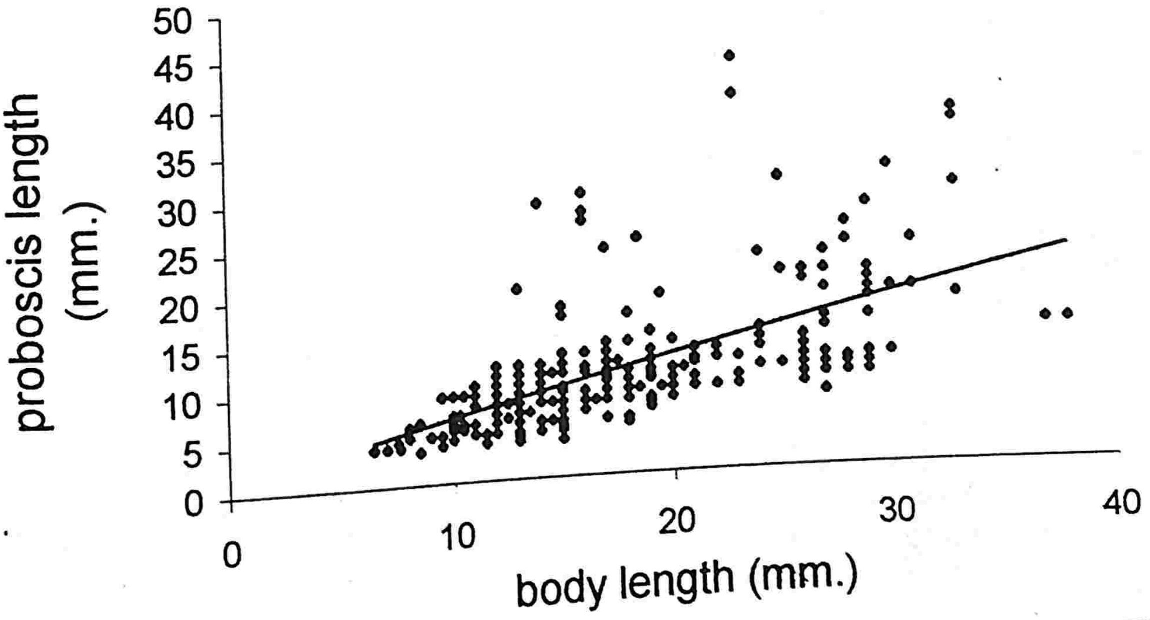


FIG. 9. SOCIABLE HOST HYPOTHESIS.

SOCIABILITY

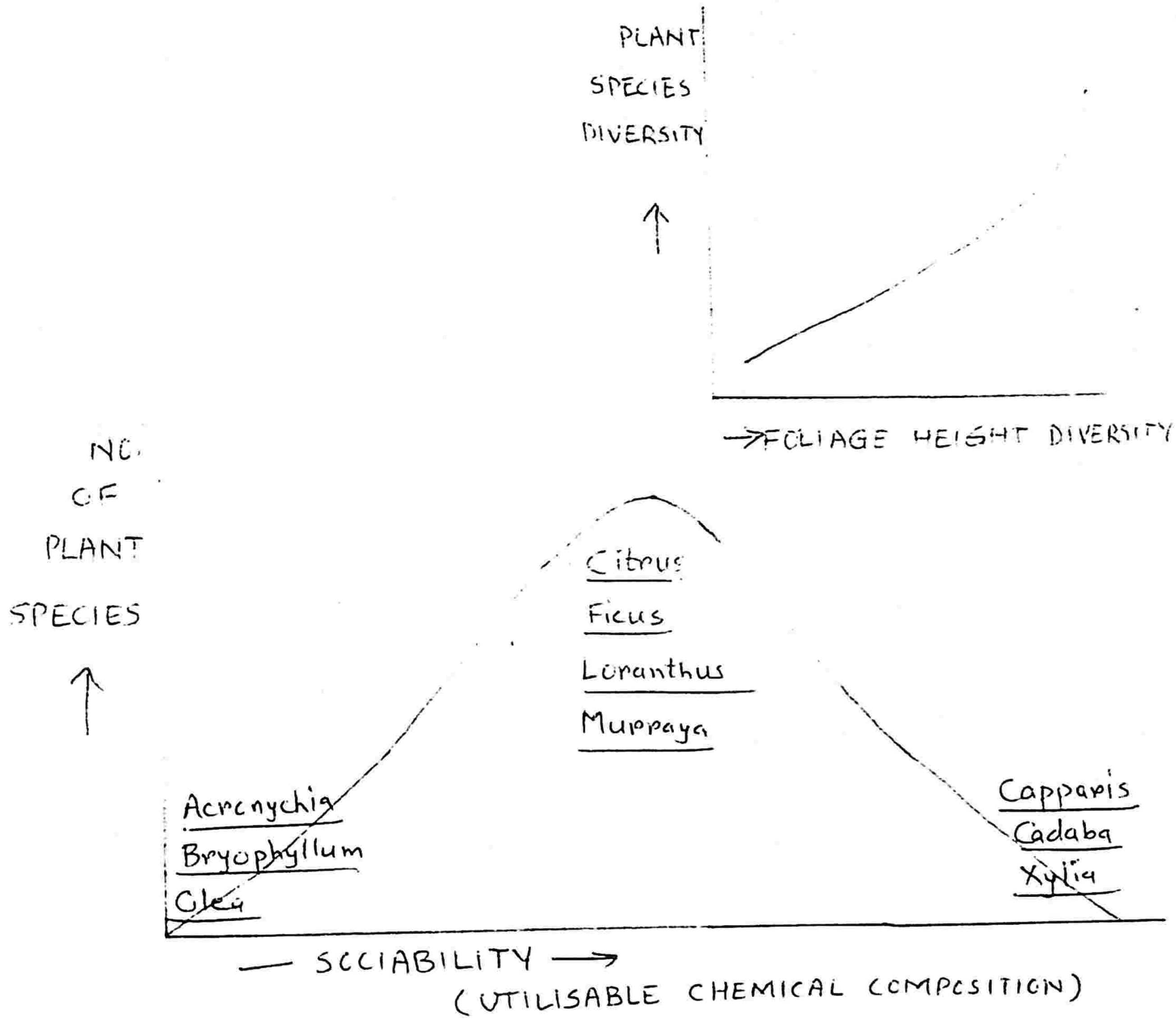
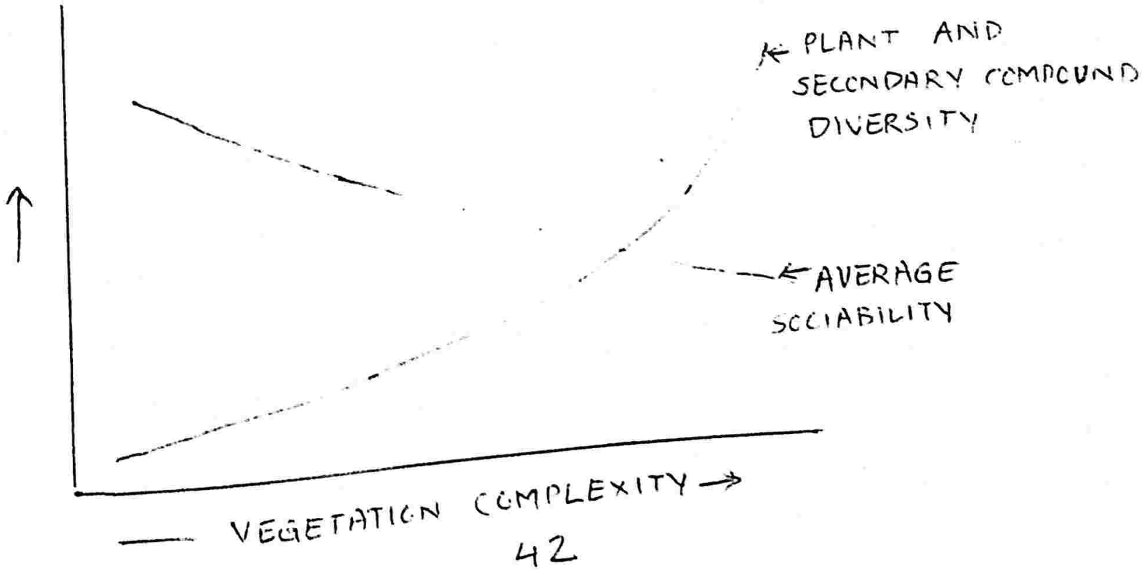


FIG. 10. SOCIABLE HOST HYPOTHESIS

THE HYPOTHESIS.



APPENDIX ~~2~~ 1. HABITAT USE OF BUTTERFLIES IN THE ANAMALAIS, SOUTH INDIA

SR. NO.*	BUTTERFLY SPECIES COMMON NAME	VEGETATION TYPES EVG.	SHOLA	DECE.	BAMB.	TEAK	SCRUB	SAVAN.	GRASS.	STRATUM USE 0-10m.	10-25m.	>25m.
	FAMILY PAPILIONIDAE											
1	SOUTHERN BIRDWING	+	+	+	+	+				+	+	+
2	MALABAR OR CEYLON ROSE	+		+						+	+	
3	COMMON ROSE	+	+	+	+	+	+			+	+	
4	CRIMSON ROSE	+	+	+	+	+	+			+	+	
5	COMMON BLUEBOTTLE	+	+							+	+	+
6	COMMON JAY	+	+	+						+	+	+
7	TAILED JAY	+	+							+	+	+
8	SPOT SWORDTAIL			+		+				+	+	
9	FIVE-BAR SWORDTAIL	+								+	+	
10	COMMON MIME			+	+	+				+	+	
11	LIME	+	+	++	++	+	+			+		
12	MALABAR BANDED SWALLOWTAIL	+								+	+	
13	MALABAR RAVEN	++	+	+	+					+	-	
14	RED HELEN	++	+	+						+	+	
15	COMMON MORMON	+	+	+	+	+	+			+	+	
16	BLUE MORMON	++	+	+	+	+				+	+	
17	PARIS PEACOCK	+	+							+	+	+
19	COMMON BANDED PEACOCK					+	+			+		
	FAMILY PIERIDAE											
20	COMMON EMIGRANT			++	+	+	+			+	+	
21	MOTTLED EMIGRANT			+		+	++	+		+	+	
22	SMALL GRASS YELLOW			+	+	+	+	+		+		
23	SPOTLESS GRASS YELLOW			+	+	+	+	+	+	+		
24	COMMON GRASS YELLOW	+	+	++	+	+	+	+		+	?	?
25	THREE-SPOT GRASS YELLOW	++	+	+	+	+				+	+	+
27	NILGIRI CLOUDED YELLOW		EDGE +							+		

* SR. NO. CORRESPONDS TO THE SPECIES NO. IN APPENDIX 1.

28 COMMON JEZEBEL	+	+	+	+	+	+			+	+	+
29 PSYCHE			+	+	+	+			+		
31 INDIAN CABBAGE WHITE		EDGE +							+		
32 COMMON GULL			+	+	+	+			+	+	
33 LESSER GULL	+								+	+	
34 PIONEER OR CAPER WHITE			+	+	+	+	+		+	+	
35 PLAIN PUFFIN	++	+							+	+	+
35a SPOT PUFFIN		EDGE +							+	+	+
36 STRIPED ALBATROSS					+	+			+		
37 CHOCOLATE ALBATROSS	+		+	+	+	+			+	+	
38 COMMON ALBATROSS	++	+	+	+	+	+	+		+	+	+
39 LESSER ALBATROSS	++	+	?	?	?				+	+	+
40 SMALL SALMON ARAB						+			+		
41 SMALL ORANGE TIP						+			+		
42 PLAIN ORANGE TIP						+			+		
43 CRIMSON TIP						+			+		
48 YELLOW ORANGE TIP			+		+	+			+		
49 COMMON WANDERER			+						+		
50 DARK WANDERER	+								+		
51 GREAT ORANGE TIP			+	+	+				+	+	+

FAMILY NYMPHALIDAE

54 COMMON EVENING BROWN	++	+	+	+	+				+	+	
55 GREAT EVENING BROWN	+	+	+						+	?	
56 DARK EVENING BROWN	+		+	+					+	?	
57 COMMON PALMFLY	+								+	+	+
58 BAMBOO TREEBROWN			+	+					+	?	?
59 TAMIL TREEBROWN	+	+	+	+	+				+	+	+
60 COMMON TREEBROWN		+	+	+					+	?	?
61 WHITEBAR BUSHBROWN	+	+							+		
62 BUSHBROWNS	++	+	+	+	+	+	+		+		
68 GLADEYE BUSHBROWN	+		++	++	+				+		
69 RED-DISK BUSHBROWN		+						+	+	+	?
72 NIGGER			+	+					+		

44

75 WHITE OR CEYLON FOURRING			+			+			+		
76 COMMON FOURRING			+	+	+	+	+		+		
78 COMMON FIVERING	EDGE +	EDGE +	+	+	+				+		
81 PALNI FOURRING								+	+		
82 COMMON NAWAB			+		+				+	+	
85 TAWNY RAJAH	+		+						+	+	
87 TAWNY COSTER			+		+	+			+		
88 TAMIL LACEWING	+		+						+	+	
89 CRUISER	+								+	+	
90 RUSTIC	+	+	+	+					+	+	+
91 COMMON LEOPARD	+	+	+	+	+				+		
93 TAMIL YEOMAN	+	+	+						+	+	+
94 INDIAN FRITILLARY		EDGE +						+	+	+	
95 BLACK PRINCE	+	+							+		
97 CHESTNUT-STREAKED SAILOR	+	+	+	+	+				+	+	+
98 COMMON SAILOR	+	+	+	+	+	+	+		+	+	+
102 YELLOWJACK SAILOR	+								+	?	?
103 SHORTBANDED SAILOR	+	?	+						+	+	+
104 COMMON LASCAR	+		++	+	+				+	+	
108 BLACKVEIN SERGEANT	+	?							+	+	+
109 COMMON SERGEANT			+				+		+		
110 COMMANDER	+	+	+						+		
111 CLIPPER	++	+	+						+	+	+
112 GREY COUNT	+	+	+	+					+	+	?
114 COMMON BARON	++	?	+						+	+	?
117 REDSPOT DUKE	++	+							+	+	+
119 ANGLED CASTOR	EDGE +	EDGE +	+	+	+	+	+		+		
120 COMMON CASTOR			+	+	+				+		
121 COMMON MAP	+	+							+	+	?
124 YELLOW PANSY			+	+	+	+	+	+	+		
126 LEMON PANSY	EDGE +	EDGE +	+	+	+	+	+		+		
128 GREY PANSY	SWAMP+		SWAMP+						+		
129 CHOCOLATE PANSY	+	+	+	+	+		+		+	+	
130 PAINTED LADY	+	+	+			+	+	++	+		
131 INDIAN RED ADMIRAL		+						+	+	+	

132 BLUE ADMIRAL	+	+	+						+	+	
133 GREAT EGGFLY	+	+	+	+	+				+	+	
134 DANAID EGGFLY			+	+	+	+			+	+	
138 GLASSY TIGER	++	+	++	+	+				+	+	+
139 NILGIRI TIGER	STRAY+	++						+	+	+	+
140 BLUE TIGER			+	+	+				+	+	
141 DARK BLUE TIGER	++	+	+	+	+	+	+		+	+	+
142 PLAIN TIGER						+			+		
143 STRIPED OR COMMON TIGER			+	+	+	+			+		
144 COMMON INDIAN CROW	+	+	+	+	+	+	+		+	+	+
145 DOUBLE-BRANDED CROW	+	?	+						+	+	+
147 MALABAR TREE NYMPH	+								+	+	
FAMILY LYCAENIDAE											
148 PLUM JUDY	++		+	+					+		
149 APEFLY			+						+		
151 COMMON PIERROT			++	+	+	+			+		
152 ANGLED PIERROT	+	+	+	+					+		
153 BANDED BLUE PIERROT	+	+	+	+					+	+	
154 DARK PIERROT	+	+	+	+	+				+		
159 ZEBRA BLUE			+	+	+				+	+	
163 INDIAN CUPID								+	+	+	
164 WHITE HEDGE BLUE	+	++	+						+	+	
165 SINGALESE/LARGE HEDGE BLUE	?								+		
166 COMMON HEDGE BLUE	+		+	+	+				+		
169 PLAIN HEDGE BLUE	+								+		
170 QUAKER	+								+	?	
171 MALAYAN	+	?							+	?	
172 PALE GRASS BLUE						+			+		
173 DARK GRASS BLUE			+	+	+	+			+		
174 LESSER GRASS BLUE			+	+	+	+			+		
175 TINY GRASS BLUE	+	+	+	+	+	+			+		
179 GRASS JEWEL						+	+		+		
180 GRAM BLUE			+	+	+	+	+		+		

181 FORGET-ME-NOT			++	+	+				+		
183 PEA BLUE			+	+	+	+	+	+	+		
184 DARK CERULEAN	+	+	+	+	+				+		
185 COMMON CERULEAN	+	+	+	+	+				+	+	
186 METALLIC CERULEAN	+	?	+						+		
187 LINE BLUE SPP.	+	+	+	+					+	+	+
198 RED PIERROT			+	+	+	+			+		
200 POINTED CILIATE BLUE	+	+	+	+	+				+	?	?
201 OAKBLUE SPP.	+								+		
207 MANYTAILED OAKBLUE	+								+	+	?
210 SILVERSTREAK BLUE	+								+	+	+
211 LEAF BLUE	+								+		
212 COMMON SILVERLINE	+	+	+	+					+		
215 SCARCE SHOT SILVERLINE						+			+		
220 COMMON TINSEL			+			+			+	+	
221 YAMFLY	+		+	+					+		
222 COMMON IMPERIAL	++	?	+						+	+	?
223 MONKEY PUZZLE	+								+		
224 COMMON ONYX	+									+	
229 ROYAL SP.			+						+	+	?
234 BANDED ROYAL			+		+				+	+	
238 CORNELIAN	+		+						+	+	
242 INDIAN RED FLASH		+	+			+			+		
244 SLATE FLASH	+		+						+	+	
245 INDIGO FLASH	+								+	+	
246 SUNBEAM SP.			+		+	+			+		
FAMILY HESPERIIDAE											
252 COMMON BANDED AWL			+						+		
253 WHITE BANDED AWL	+	+							+	+	?
256 BROWN AWL	+		+	+	+				+	+	
258 COMMON SPOTTED FLAT	+	+	+						+	?	
260 TAMIL SPOTTED FLAT		+							+	+	
261 COMMON SNOW FLAT	++	+	+	+					+	+	

262 SUFFUSED SNOW FLAT	++	+	+	+					+	+	
263 WATER SNOW FLAT	++	+							+	+	
265 FULVOUS PIED FLAT	EDGE +	+	+	+	+				+	+	
267 COMMON SMALL FLAT			+	+	+	+			+		
270 CHESTNUT/BANDED ANGLE			+		+				+		
271 GOLDEN ANGLE			+	+					+		
275 INDIAN SKIPPER						+	+		+		
277 DINGY SCRUB-HOPPER		EDGE +						+	+		
278 BUSH HOPPER			+						+		
286 CHESTNUT BOB	++	+	+	+	+				+		
287 COON	++			+	+				+		
288 COMMON BANDED DEMON	+								+		
289 RESTRICTED DEMON	++		+	+	+				+		
291 GRASS DEMON					+	+			+		
296 WAX DART			+		+				+		
300 YELLOW-BASE TREE FLITTER	++	+							+	?	
301 GIANT REDEYE	+	+							+	+	?
305 TAMIL GRASS DART						?	+		+		
307 INDIAN/COMMON DARTLET	+								+	+	
308 DART SPP.	+								+	+	
313 PALE PALM DART			+	+			+		+		
314 DARK PALM DART			+	+			+		+		
325 CONTIGUOUS SWIFT	EDGE +	EDGE +							+		
TOTAL SPECIES IN THE HABITAT	108	75	117	79	73	52	24	11	178	86	29

1.This appendix gives vegetation-type-wise list of butterfly species that I saw in Anamalais during November 1998 to May 1999. Serial numbers behind the species names are the species numbers from Gaonkar (1996).

2. Details of the vegetation types are given in the thesis (section 2.2).

3. Presence-absence of a butterfly species in a vegetation type is based mainly on my field observations, and from judgement of the habitat of the larval host plant(s) of the butterfly species.

4. Stratum use by butterflies is based on my direct observations during usual butterfly counts, as well as during the canopy sampling.

5. A + sign indicates presence of the butterfly species in a vegetation type or horizontal vegetation stratum. A ++ sign indicates preference for that category. A "?" means that I have an unconfirmed sighting of the butterfly species in the vegetation type or horizontal stratum, but most probably it does occur in the habitat.

6. Common English names of the butterfly species in this list, and their scientific names, follow: a) Gaonkar, H. 1996. Butterflies of the Western Ghats: with notes on those of Sri Lanka. Centre for Ecological Sciences, Zoological Museum (Copenhagen) and Natural History Museum (London). b) Larsen T. B. 1987-88. The butterflies of the Nilgiri mountains of southern India (Lepidoptera: Rhopalocera). *J. Bombay Nat. Hist. Soc.* 84(1-3):26-54, 291-316, 560-584, and 85(1):26-43; and c) Wynter-Blyth, M. A. 1957. The butterflies of the Indian Region. Bombay Natural History Society-Oxford University Press.