CHAPTER IV

FEEDING ECOLOGY OF THE SUMATRAN RHINOCEROS IN SOUTHERN PENINSULAR MALAYSIA

ABSTRACT

Feeding ecology of the Sumatran rhinoceros in the Endau-Rompin region, southern Peninsular Malaysia, was studied during 1979 through 1981 to provide information on foods eaten and habitats selected. Feeding sites were located by following recent rhino tracks. Within primary hill forest, Sumatran rhinos selected feeding sites in stream bottom (59%) and lower slope (34%) physiographic types. Small forest gaps (35%) were used more than their availability (15%), but most of the feeding cases were in closed-canopy forest (63%). Sumatran rhinos were mostly browsers, feeding primarily on the mature leaves of woody understory plants. Large, fleshy fruits were eaten occassionally. The diet was diverse with 49 plant families, 102 genera, and between 156 to 181 species represented in 342 feeding cases. *Prunus* sp. (15.1%), *Ficus* sp. (6.4%), *Medusanthera* sp. (3.8%), and *Eugenia* sp. (3.0%) contributed the greatest amounts to diet proportions based on total bites (11,818). Chemical analyses of plant materials, collected from certain food plants and randomly selected non-food plants, indicated that Sumatran rhinos selected plants and plant parts that were high in mineral and crude protein content but low in fiber. Phenolics and tannins were tolerated in the diet, but principal food plants contained less condensed tannin. Rhino feeding behavior was influenced by forage quality, the availability of foods and habitat attributes, and feeding adaptations.

INTRODUCTION

The Sumatran or two-horned Asiatic rhinoceros (Dicerorhinus sumatrensis Fisher 1814) is the only extant rhinoceros living entirely in primary tropical rain forest habitats. The feeding ecology and habitat relationships of this unique species, along with most other large terrestrial herbivores in tropical rain forest habitats, are poorly understood. Rare secretive animals, complex plant communities, and difficult working conditions have discourged most field researchers. In tropical Asia, conservation and management programs have suffered from the lack of basic information on the ecological relationships between wildlife and habitat (Stevens, 1968; Lee, 1980). As many of the large mammals slip toward extinction (Simon, 1969), the impacts of habitat modification and destruction on wildlife need evaluation.

In 1974, the Malaysian Department of Wildlife and National Parks (DWNP) initiated a long-term study on the status and ecology of the Sumatran rhinoceros in Peninsular Malaysia (Flynn, 1978). Early investigations determined that the Endau-Rompin area, located in southern Peninsular Malaysia, contained the largest population of Sumatran rhinos remaining in the country, about 20 to 25 individuals (Flynn and Abdullah, 1983a). In this paper, I present an analysis of feeding ecology and habitat selection by the Sumatran rhino in the Endau-Rompin region. The study's objectives are as follows: 1) to determine the kinds and relative amounts of foods eaten; 2) to describe the habitats selected for feeding; 3) to compare the use of foods and habitats with their availability within the study area; and 4) to investigate the relationships between plant chemistry and food selection.

The Sumatran rhino is the smallest and most primitive rhinoceros (Groves and Kurt, 1972). Adults probably weigh up to 1000 kg with shoulder heights to 1.45 m. Both sexes have a short nasal horn and an inconspicuous frontal horn. Sometimes the body is covered by hair, largely disappearing with age. The skin folds are striking features, one encircling the trunk just behind the fore-legs and another on the belly and flanks, but not on the back, just before the hind-legs. The pair of upper incisors have large flattened crowns, and the enlarged pair of lower canines have been modified into sharp forward pointing tusks (Groves, 1967). The pre-molars and molars are similar and relatively low crowned with tranverse ridges of enamel, indicating a non-specialized browsing habit. Once found across Southeast Asia, this rare forest-dwelling rhino is now restricted to small isolated populations in Burma, Thailand, the Malay Peninsula, Sumatra, and Borneo (Van Strien, 1974; McNeely and Laurie, 1977; Borner, 1978; Andau and Payne, 1982; Flynn and Abdullah, 1983b). Historic hunting of rhinos for the believed medicinal values of their body parts has greatly depleted numbers (Van Strien, 1974; Martin, 1979); extensive habitat destruction by logging and forest clearance for agricultural development has reduced the amount of suitable habitat and isolated already small populations (Flynn and Abdullah, 1983b).

The rhinoceroses (Perissodactyla: Rhinocerotidae) are of special interest in the study of feeding ecology because of their colonic/cecal digestive system (Foose, 1982). Recently, the relative advantages and adaptations of the ruminant and nonruminant digestive systems have received some investigation (Janis, 1976; Parra, 1978; Foose, 1982; Van Soest, 1982). The ruminant system appears adapted to maximize the extraction of energy and protein per unit of vegetation consumed, but the reticulo-omasal orifice retards the passage of fibrous particles through the gut (Van Soest, 1982). In the hindgut or nonruminant digester, the site of microbial fermentation is located after the normal sites of mammalian digestion and absorption in the stomach and small intestine (Janis, 1976; Parra, 1978; Foose, 1982). Most soluble carbohydrates and proteins are digested prececally by enzymatic action, but fibrous materials are fermented by microbial activity in an enlarged colon and/or prominent cecum (Parra, 1978). Nonruminants appear to maximize the extraction of nutrients per unit time by faster passage rates and larger intakes of forage; they minimize nutrient requirements per unit weight by enlargement of their body sizes (Janis, 1976; Foose, 1982).

A herbivorous life-style presents many problems for an animal. Plants are not just food for animals; they have evolved protective systems to ensure their own continued existence and survival (see Rosenthal and Janzen 1979). Plant protective systems include physical and chemical structures that resist attacks by leaf predators. Physical protective strategies commonly include thorns, hairs, or other physical modifications of the leaves or stems, enlarged height and size of stems, and unpredictability in time and/or space. The plant chemical world is vast and complex, often poorly understood (Janzen 1978). Herbivores extract plant chemicals for nutrients by digestive processes, but often vegetation is a poor food packet. Nutrients may have positive or negative value to the herbivore after ingestion (Freeland and Janzen, 1974; Westoby, 1974). Proteins, soluble carbohydrates, and most minerals are common positive nutrients required by an animal for growth, maintainence, and reproduction. In addition, plants synthesize a vast array of secondary metablolites that have negative impacts on herbivores. Secondary plant compounds can be grouped as digestion-reducing compounds or plant toxins (Rhoades and Cates 1976). Digestion-reducing compounds often have a quantitative (dosage-dependent) effect because they complex with proteins and animal enzymes, interfer with animal metabolism, or inhibit gut microfloras (Freeland and Janzen, 1974; Feeny, 1976; Rhoades and Cates, 1976; Bryant, 1981; Becker, 1982). Phenolic compounds, such as phenolic acids, flavonoids, and tannins, are included in this group (Levin, 1971; McKey et al., 1978). Plant structural carbohydrates, such as cellulose and lignin, are undigestible by mammalian enzymatic action. Cellulose can be degraded by microbial fermentation; lignin is totally undigestible and limits the availability of cell wall carbohydrates to digesting microbes (Van Soest, 1982). Plant toxins include a wide range of plant chemicals that act as poisons. These chemicals are generally active in small quantities and extremely toxic once they enter the herbivore´s body (Freeland and Janzen, 1974; Rhoades and Cates, 1976).

Alkaloids and saponins are characteristic of this group (Levin and York, 1978; Rosenthal and Janzen, 1979).

Before this study, little quantitative information on the foods and habitats selected by this unique species was available. Previous papers have contained only lists of plants recorded as eaten or observations of habitats used (Van Strien, 1974). In Malaysia, Hubback (1939) recorded 44 plant taxa as rhino food plants; most of the information was collected while he hunted them in the hill forests of central Pahang. Additional plant taxa were provided by Strickland (1967) from a 1-year study conducted in the west-coastal lowland forests of Sungei Dusun Wildlife Reserve. Borner (1978) and N. Van Strien (pers. comm.) have compiled extensive lists of plants eaten by Sumatran rhinos in the mountainous rain forests of Gunung Leuser Reserve, northern Sumatra. Only limited information from incidental observations has been available from the monsoonal forests of Thailand and Burma (Evans, 1905; Thom, 1935; Talbot, 1960).

STUDY AREA

Investigations were conducted at the Selai River study site in the Endau-Rompin region, a proposed national park of over 870 km^2 located in southern Peninsular Malaysia (2° 30′ N, 103° 15′ E). I defined the study area as the portion of the upper Selai River watershed lying west of 103° 12′ E longitude, an area of about 40 km^2 (Fig. 1).

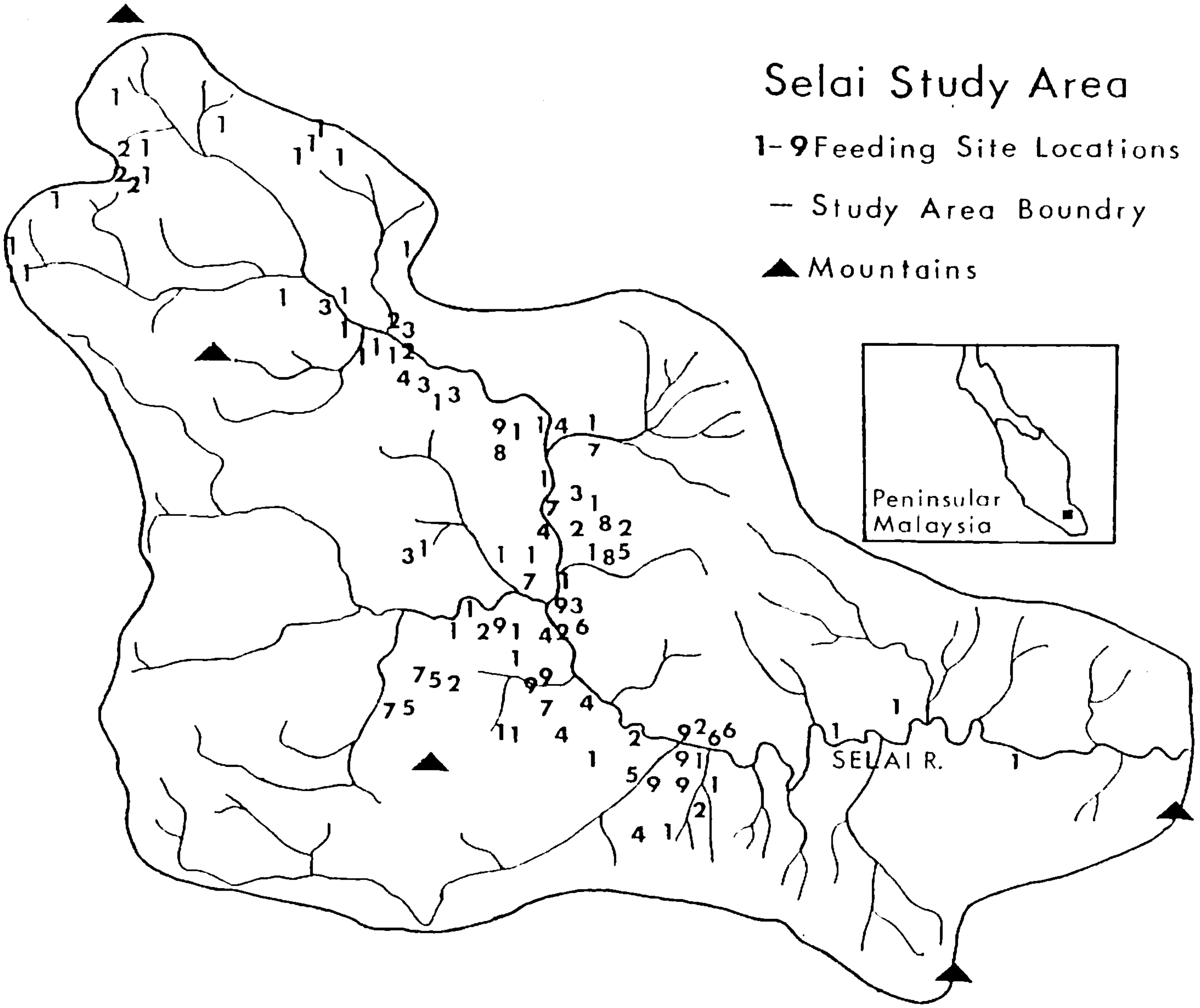

Fig. 1. Selai River study area located in the Endau-Rompin region, southern Peninsular Malaysia. Sumatran rhino feeding site locations are marked by the numbers 1 to 9. The numerical value indicates the number of feeding sites at the location.

The only access to this remote site was by foot travel along a forest path from the end of the nearest road, 10 km west of the research camp.

The topography of the study area is generally hilly, locally quite steep, and dominated by a north-south trending mountain range. Within the study area, the upper Selai watershed forms a distinct high basin on the east side of the main mountain range. Adjacent to the eastern boundary of the study area, the Selai River drops abrubtly 300 m over the next 1.6 km. Elevations vary from 350 m along the stream to 900 m at the highest point. The mountains are composed of undifferentiated granitic rocks of Triassic age; Permian volcanic rocks of andesitic and rhyolitic composition occur in the eastern section (Gobbett and Hutchison, 1973). The soils are quite variable depending on the underlying parent material, but they are generally of poor quality (Smallwood, 1966). Red and yellow latosols and podzolic soils derived from acid igneous rocks cover most of the area. Latosals and podzolic soils derived from sedimentary rocks are found farther to the east.

The climate is characteristic of the moist tropics, uniformly warm and humid throughout the year. Although accurate weather information was not available for the study site, seasonal variation in temperature and rainfall was slight. At a nearby lowland site (Segamat), the mean daily temperature was 27° C, with the diurnal range greater than the seasonal range (Dale, 1963). The mean temperature at the Selai base camp, elevation 470 m, was 24° C. Typically, the relative humidity was near 100% in the forest understory. Rainfall was abundant throughout the year, except for a slight decrease during the January-to-May intermonsoonal period. Annual mean rainfall was extrapolated to be near 2800 mm, based on records from nearby lowland stations at the interior town of Segamat (2000 mm) and the coastal town of Mersing (3300 mm) (Dale, 1959).

The natural vegetation of the study area is tropical evergreen rain forest of the Indo-Malayan formation (Richards, 1952; Whitmore, 1975). These forests are the world's most luxuriant and species-rich; an estimated 4100 species of woody plants occur in Peninsular Malaysia (Whitmore, 1972; 1975). In general, these forests are characterized by numerous large, evergreen, broad-leafed trees with a predominance of individuals from the family Dipterocarpaceae. Forest structure is characterized by a few large emergent trees, a nearly closed canopy at about 25 m, and an understory consisting of numerous seedlings and juveniles of large trees, shrubs, palms, climbers, and herbaceous plants. Successional dynamics of tropical rain forests are characterized by the death and collapse of large forest trees, creating small gaps in the canopy (Whitmore, 1975). These gaps are filled by juvenile trees growing in the understory or by invading species. As these understory trees grow to maturity, the gap is closed and the rebuilding forest returns to the mature, closed-canopy phase. Many problems exist in the classification of tropical rain forest communities (Poore, 1963), but several general forest types are recognized (Wyatt-Smith, 1964; Forest Department, 1977). Most of the study area is covered with mixed hill dipterocarp forest. According to Gyekis (1966), the western portion consists of meranti-keruing mixed hill forest with seraya-keruing hill forest on the ridges and well-drained upper sites.

In addition to the Sumatran rhinoceros, the large mammal fauna of the Endau-Rompin region includes elephant (*Elephas maximus*), Malayan tapir (*Tapirus indicus*), gaur (*Bos garus*), bearded pig (*Sus barbatus*), common pig (*Sus scrofa*), mouse deer (*Trangulus napu*, T. *Javanicus*), barking deer (*Muntiacus muntjak*), sambur deer (*Cervus unicolor*), common leopard (*Panthera pardus*), and tiger (*Panthera tigris*).

METHODS AND MATERIALS

Feeding Behavior

A system of foot paths was cut through the forest understory in the study area, and 2 base camps were built at points located 12 and 20 km from the end of the nearest road. I searched the study area for rhino tracks along the trail system from the base camps using skilled animal trackers hired from the nearby village of Kampung Juaseh. Additional field staff were provided by the Malayan Department of Wildlife and National Parks (DWNP). Once a set of recent tracks had been located, the rhino´s trail was followed and all evidence of feeding activity was recorded. Each individual plant that had been eaten by a rhino was treated as a case of feeding, or a feeding site. Rhino feeding behavior was studied by recording evidence of their feeding activities left at feeding sites. Method of feeding was described in terms of pushing or breaking the plant's main stem. The amount of plant material eaten from each plant was estimated using a bite-count method similar to Peek et al. (1976). A standard rhino bite consisted of a 10 cm length of leaf or stem material. The number of bites removed from a plant was estimated by carefully examining branches of the plant that had not been eaten. The total number of bites available at a plant was calculated by adding the number of bites remaining on a plant to the number of bites estimated to have been consumed. The mean weight of a standard bite was calculated by measuring the weight of 100 bites of individual leaves from 10 species of trees and 50 bites of stem from 5 different trees. The mean weight of leaf material was found to be 2.4 g and stem 1.4 g.

The distance between feeding sites was measured by recording the number of steps taken between them with a hand counter. I estimated my average step length at 1 m and converted the number of steps to linear distance.

Food Plant Characteristics

A leaf sample was collected from each plant recorded as eaten by a rhino at a feeding site for later identification. Also, the local common name was noted for each plant. The leaf samples were pressed over night, then sealed in a plastic bag with ethanol (Womersley, 1969) until delivered to the the Forest Research Institute (FRI), Department of Forestry, Kepong, Malaysia, for identification. Mr. K. M. Kochummen and Dr. F. S. P. Ng kindly arranged for the identifications of all the plant materials. The plant life form - woody sapling, climber, palm, or herbaceous plant - was recorded for each plant. Also, each stem was examined for the presence of thorns or other physical defense structures and measured for diameter at breast height (DBH) and total height.

The ecological characteristics of rhino food plants were investigated by reviewing the available literature, primarily Van Steenis (1953), Whitmore (1972), Wyatt-Smith and Kochummen (1979), and K. Kochummen (pers. comm.). Plant taxa were evaluated in terms of their typical canopy position, forest type, successional stage, and timber potential.

Habitat Characteristics

Habitat attributes were measured at each feeding site to obtain quantitative information on the habitat characteristics selected for feeding. The habitat was evaluated in terms of physiographic type, elevation, slope, successional stage, and canopy cover. At each feeding site, the plant that had been eaten by a rhino established the center point for a circular plot with a diameter of 20 m. The map grid location and elevation were determined from topographic maps available from the Malaysian Government Printing Office. Based on topographic and slope characteristics, the site was placed into 1 of 4 physiographic types, as follows: 1) stream bottom - level land along the stream's flood plain; 2) lower slope - gently sloping land adjacent to the flood plain; 3) upper slope - steeply sloping land above the lower slope type; and 4) ridge - gently sloping land along the top of the ridges. A measure of slope was obtained by ocular estimate and expressed as a percent. Successional stage of the forest at a feeding site was categorized as either closed canopy (mature forest), new gap, old gap, or open riverine (disturbed). In the new gap phase, a large forest tree had recently fallen, creating an opening in the forest canopy. In contrast, the old gap phase had a new generation of seedlings growing in the opening. Open areas along the major streams were classified as open riverine. Canopy cover was measured by taking 20 sightings at 1 m intervals directly above the plot through an ocular tube and recording the presence or absence of canopy at each sighting (James and Shugart, 1970). Canopy cover was expressed as the percentage of the sightings with canopy present. The general forest type was determined by the presence of indicator species nearby.

Habitat Availability

Transects. Information on the vegetative characteristics of the study area was gathered from 14 transects. The 4 physiographic types were delinated on a topographic map, and the starting points for 4 transects were randomly placed in each type, except ridge (2 transects). Each transect, laid out along a compass bearing parallel to the longest axis of the habitat patch, was 400 m long and divided into 20 points at 20 m intervals. Each point along the transect line was treated as a potential feeding site and described in the same manner. Information was recorded on canopy cover, successional stage, and slope.

Woody saplings within the rhino food plant size class (stem DBH between 0.8 and 3.2 cm) were enumerated along each transect using the point-center quarter method (Mueller-Dumbois and Ellenberg, 1974). At each point, the plot was divided into 4 quarters by a line perpendicular to the transect line. The distance to the nearest woody sapling between 0.8 and 3.2 cm DBH was recorded for each quarter. The local name was noted for each sapling. The amount of leaf material in the forest understory was determined by estimating the total number of bites of leaf available at each sapling. In addition, phenology of the woody saplings was determined by recording the number of bites of young and mature leaves present on each plant.

Random points. Certain habitat attributes were more easily measured by placing random points on a map of the study area with the habitat types delineated (Marcum and Loftsgaarden, 1980). Using a 100 m grid of the study area, the x, y coordinates of 100 random points were generated by a computer program (P. Conry, pers. comm.). The elevation and physiographic type were recorded from the map for each random point. The proportions of the study area occupied by the 4 physiographic types and the mean elevation of the study area were adequately estimated by 100 random points.

Plant Chemistry

Food plants. Information on the chemical composition of food plants was obtained from the analysis of leaf or stem material collected from plants eaten by the rhinos. Samples consisted of 20-30 g (fresh weight) of a single plant part (young leaf, mature leaf, or stem) taken from an individual plant that had been eaten by a rhino at a feeding site. Most of the samples were collected from a few long feeding bouts during February through May 1981. I attempted to collect samples from every plant that had been eaten by a rhino during a feeding bout, thus including plants that showed various levels of use. Because the plants could not be identified at the time of collection, the plant taxon of a sample was not known until the chemical analyses had been completed. Collected materials were initially held in sealed plastic bags. After returning to camp, each sample was heated in a portable kerosene oven at 50 to 60° C for at least 1 hour, then allowed to air-dry in open bags until delivered to a laboratory. At Highlands Research Unit, Kelang, Malaysia, the plant samples were oven-dried at 55° C, then ground to pass through a 1 mm screen.

The total content of selected mineral elements and nitrogen (N) were assessed in all samples by Highlands Research Unit following standard procedures. The N content was determined by the Kjeldahl method and estimates of crude protein obtained from N x 6.25. Phosphorus (P) content was determined using Vanando-Molybdate calorimetry, potassium (K) using a flame photometer, and calcium (Ca) and magnesium (Mg) using an atomic absorption spectrophotometer. The dried plant material remaining from the previous asssays was sealed in plastic bags, then shipped to the Phytochemistry Research Laboratory, University of Strathclyde, UK. Dr. P. Waterman assayed these samples for total phenolic content (TP), condensed tannins (CT), and acid detergent fiber (ADF) (Waterman et al., 1980). All chemical parameters were expressed as percent dry weight.

Non-food plants. Mature leaf material was collected from the nearest non-food plant at alternate points along 3 of the vegetative transects, 1 each in the stream bottom, lower slope, and upper slope physiographic types, to use as a control for comparisons with the food plants. After these plants had been identified, all genera that composed more than 1.5% of the diet were excluded from the group, leaving a total of 27 mature leaf samples. This group probably contains non-food plants that are common in the habitat, plant taxa that are uncommon and infrequently eaten, and plants that are so rare in the habitat that they are seldom eaten. These leaf samples were handled like the food plants and assayed for the same chemical components.

Data Analyses

Data organization. The basic level of organization for most of the data collected during this study was the feeding site, each plant that was eaten by a rhino; or a randomly located plot, a potential feeding site. Information on habitat attributes and feeding activities for each feeding site was entered as an observation into a computer data file. The data were analyzed on the DECSYSTEM-2050 computer system at the Unversity of Montana Computer Center. The Statistical Package for the Social Sciences (SPSS) (Nie et al., 1975) and the BMDP Biomedical Computer Programs (Dixon and Brown, 1979) software computer packages were used extensively for data manipulation, summarization, and statistical analyses.

Habitat selection. Sumatran rhino use of habitat attributes at feeding sites was determined by calculating the proportion of feeding cases in each habitat category. Discrete variables (physiographic type and successional stage) were coded as 1, 2, 3, or 4 to reflect a gradient of increasing steepness or canopy closure. For continuous variables (canopy cover, slope, and elevation), the mean response for each was estimated from the data.

Principal components analysis (Cooley and Lohnes, 1971) was conducted on the habitat data to investigate the correlations of the habitat variables with a reduced set of independent factors (components) that account for known proportions of the total variance of the data set. The 2 principal components that contained the most variance were extracted from the correlation matrix for this analysis.

For the discrete variables, the proportionate use of each habitat attribute at feeding sites was compared to the availability of the same variable in the study area as determined by vegetative transects or random points. Habitat selection at feeding sites was defined as proportionate use of a habitat attribute significantly different than the availability of that attribute in the habitat (Petrides, 1975). The null hypothesis that the rhinos used each habitat category in proportion to its occurrence in the study area was statistically tested using a chi-squared test of homogenity (Marcum and Loftsgaarden, 1980). If the null hypothesis was accepted, I concluded that no selection for that habitat attribute had occurred at P=0.10 level of significance. Rejection of the null hypothesis indicated that selection had occurred. Using the Bonferroni approach, 90% simultaneous confidence intervals for the difference between proportionate use and availability for each habitat category were constructed. Positive selection for a habitat category was defined as proportionate use significantly greater than availability and negative selection as proportionate use significantly less than availability. For continuous data (canopy cover, slope, and elevation), the sample means for each group were compared using a 2-sample t-test.

Diet composition. Botanical composition of rhino diets was calculated as percentages of the total recorded number of bites for all feeding observations during the study period. It was assumed that no seasonal differences in diet existed. Because of problems in the identification of plant materials, diet composition was expressed in terms of plant families and genera. All plant taxa eaten by rhinos were considered as food plants. Because many of the plant taxa were eaten rarely, plant taxa contributing more than 1.5% of the diet were defined as principal food plants, or plants that the rhinos ate in greatest quantities (Petrides, 1975). A use index for each feeding site was calculated by dividing the number of bites removed by the number of bites available on the plant. This index was considered a measure of forage preference (Petrides, 1975). The proportion of fruits in the diet was not determined quantitatively because of difficulties in determining the number of fruits eaten from the forest floor. Diet proportions by plant part (young leaf, mature leaf, stem) were computed by weighting the total number of bites of each type by the weight of 1 standard bite of leaf (2.4 g) or stem (1.4 g). Food plants were characterized (physically and ecologically) by computing parameter means or proportions.

Food availability. The amount of food available in the forest understory was estimated by the enumeration of saplings along transects using the point-center quarter method (Mueller-Dumbois and Ellenberg, 1974). If the stem DBH of a woody sapling was within 1 standard deviation of the overall mean for all stems eaten (1.9 cm), the plant was considered to be available to a potential foraging rhino. The mean distance from the center point to the nearest available sapling in each quarter was computed for each physiographic type to obtain a measure of woody sapling density, expressed as stems/ha. The hypothesis that all physiographic types contained the same woody sapling density was tested with a 1-way analysis of variance (ANOVA). Scheffe´s multiple range test was used to detect differences in mean sapling density among the physiographic types (Sokal and Rolf, 1969).

The biomass of mature leaf forage available in the forest understory was estimated by multiplying the mean weight of a standard bite of leaf (2.4 g) times the mean number of bites/plant times the mean density of stems/ha for each habitat type. Because of the large standard error of such an estimate, the mean biomass of leaf material per ha was not tested for statistical differences among the habitat types.

Understory phenology was expressed as the proportion of stems with young leaf present, the mean number of bites of young leaf present, and the mean percentage of young leaf at each stem.

Diet quality. Chemical composition of rhino diets was calculated as the sum of mean forage chemical values times weighted diet percentages (Hobbs et al., 1981). For plant taxa with no chemical composition information available, the mean for the plant family was used. The intercorrelations of the plant chemistry variables were examined using principal component analysis (PCA) (Cooley and Lohnes, 1971). PCA analysis reduced the dimensionality of the problem under study, thus clarifing patterns present in the data. The first 2 principal components that contained most of the data set´s variance were extracted from the correlation matrix. Each axis was rotated by the varimax procedure to make the components more interpretable as real factors.

Food selection. Relationships between food selection and plant chemistry were examined in terms of significant differences in the chemical composition of plant taxa, or plant parts, grouped by several criteria. At the univariate level, paired t-tests were used to test differences between the chemical composition of mature leaf and stem material. A 2-sample t-test was used to test for differences in means for each variable between plant samples grouped by food and non-food plants.

Because of the multivariate nature of the data, discriminate function analysis (DFA) (Cooley and Lohnes, 1971) was used to classify the plant taxa into predetermined groups based on linear combinations of the plant chemistry variables. The first discriminant function maximizes differences among species groups, based on their chemical composition. Remaining discriminant functions account for successively smaller amounts of the difference among groups. Discriminant-function scores are orthogonal (Morrison, 1967), and because each score summarizes information from 8 parameters, the discriminant space corresponds to a "chemical hyperspace" (Garten, 1978). Because the maximum number of discriminant functions that can be derived is 1 less than the number of groups, only 1 or 2 functions were possible depending on the number of groups. For the DFA analysis, plant taxa were grouped by the following criteria: 1) principal, non-principal, and non-food plants and 2) high use index, low use index, and non-food plants.

RESULTS

Feeding Behavior

Rhino tracks were followed on 43 occasions during 25 expeditions into the study area. Often, fresh rhino tracks were difficult to locate because of the low density of animals and poor weather conditions. During some of the trips into the study area, fresh rhino tracks were not found. Often tracks were difficult to follow more than a few hundred meters, even with the assistance of a skilled native tracker. Fallen leaves obscured tracks and reduced the depth of the impression made by the animals´ toenails. Because of the time required to locate tracks and record data, tracks could be followed a maximum of 2 km a day. Thus, the distance that a particular set of tracks were followed (a feeding bout) was quite variable, ranging from 1 to 4000 m ($\bar{x}$=850 m), for a total distance of 36 km.

Altogether, 342 cases of rhino feeding were recorded during this study, an average of 7.7 cases per feeding bout. Ninety of the observations were recorded in 1979 and 252 during 1980-81. All observations for both years were pooled for the analyses because of small sample sizes and lack of significant seasonal climatic factors. Most of the data in both time periods were collected during the relatively dry months of February to May.

Method of feeding. Sumatran rhinos left obvious evidence of their feeding activities. Usually, these animals browsed only 1 individual plant at a feeding site. Thus, each plant eaten by a rhino during a feeding bout could be easily determined. Depending on a plant´s life form and size, the rhinos attacked the plant differently (Fig. 2). Short plants were browsed from above without damaging the main stem. This feeding method was observed on woody and herbaceous plants. Large woody saplings were usually pushed or the main stem broken to bring the leaves within reach of the animals´ mouths. Woody saplings with small stem diameters were broken by the animal grasping the main stem in its mouth and twisting its head sideways. Rhinos pushed saplings with large stem diameters to the ground by walking over the main stem. Sometimes, the rhinos placed their feet against the main stem, breaking it near the ground. After breaking or pushing the plant, the rhinos browswed the leaves and smaller stems, usually after walking along the main stem. Often, only leaves and stems on the upperside of the sapling were eaten. I found no conclusive evidence of animals eating bark, although this has been reported by other authors (Hubback, 1939; Strickland, 1967). In most cases where bark appeared to have been

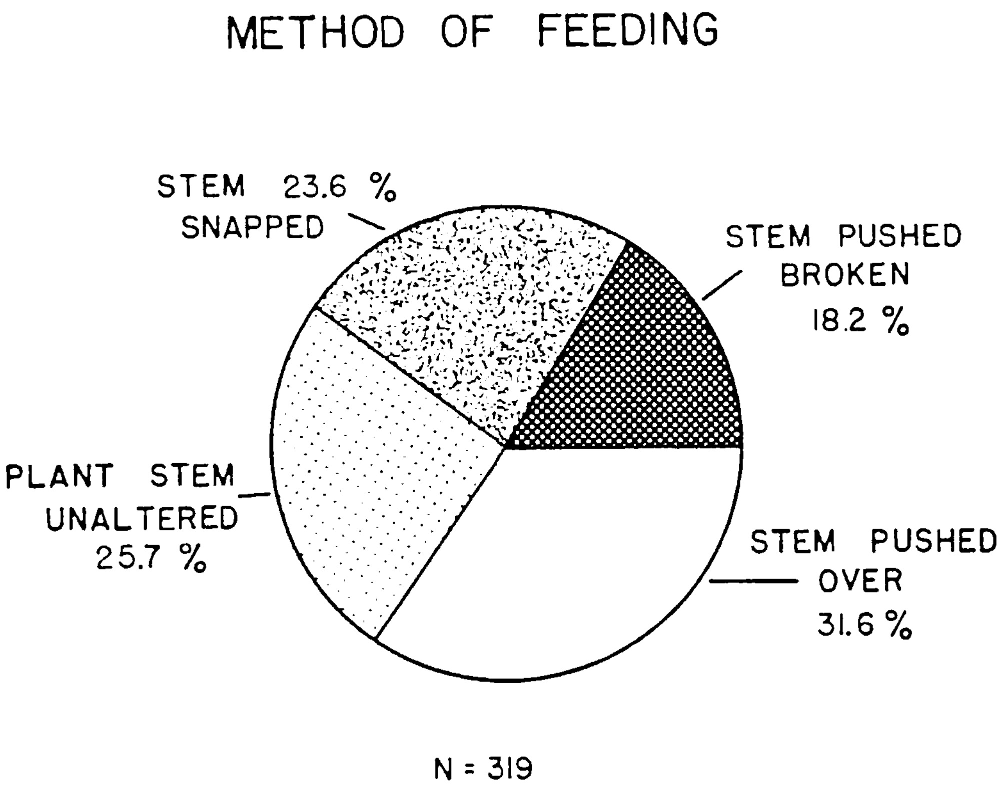

Fig. 2. Method of feeding by Sumatran rhinos on understory plants.

removed, the animal apparently rubbed the bark off with its horn or foot.

Sometimes, rhino trails led to forest trees that were fruiting. Apparently, the rhinos were eating the fruits by picking them up with their mouths, consuming them whole. This belief was supported by the presence of whole fruits in dung samples. Because of the difficulty in determing the number of fruits eaten at a site, I was unable to quantity the relative amount of fruit eaten by the rhinos.

Habitat Selection

Habitat selection by foraging rhinos was determined by an analysis of habitat attributes measured at 338 feeding sites. A principal components analysis of the habitat variables clearly showed that 2 major factors had been measured, physiography and canopy cover (Fig. 3). Physiographic type was strongly correlated with elevation, slope, and the distance from the nearest stream in the first principal component. Successional stage was strongly correlated with canopy cover in the second principal component. The first 2 principal components accounted for 76% of the variance in the data set.

A plot of the feeding site locations clearly showed the relationship with physiography. About 59% of the feeding sites were in the stream bottom type (Fig. 1), with 34% on the lower slopes adjacent to the streams. A comparison of the proportionate use of these physiographic types with their availability showed strong selection for the stream bottom and lower slope types (Fig. 4). Likewise, upper slopes were selected against. The mean elevation of feeding sites (478

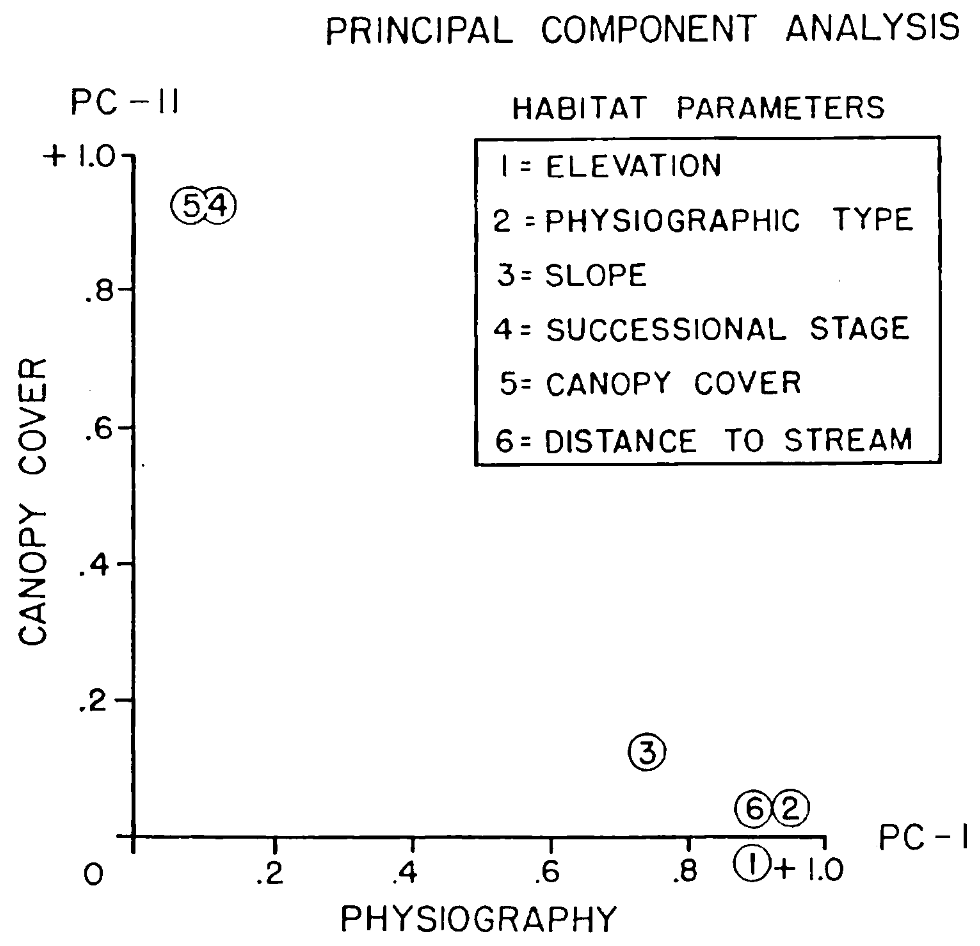

Fig. 3. Plot of the habitat parameters, measured at Sumatran rhino feeding sites, on the first 2 principal components. PC-I and PC-II contained 76% of the variance of the data set.

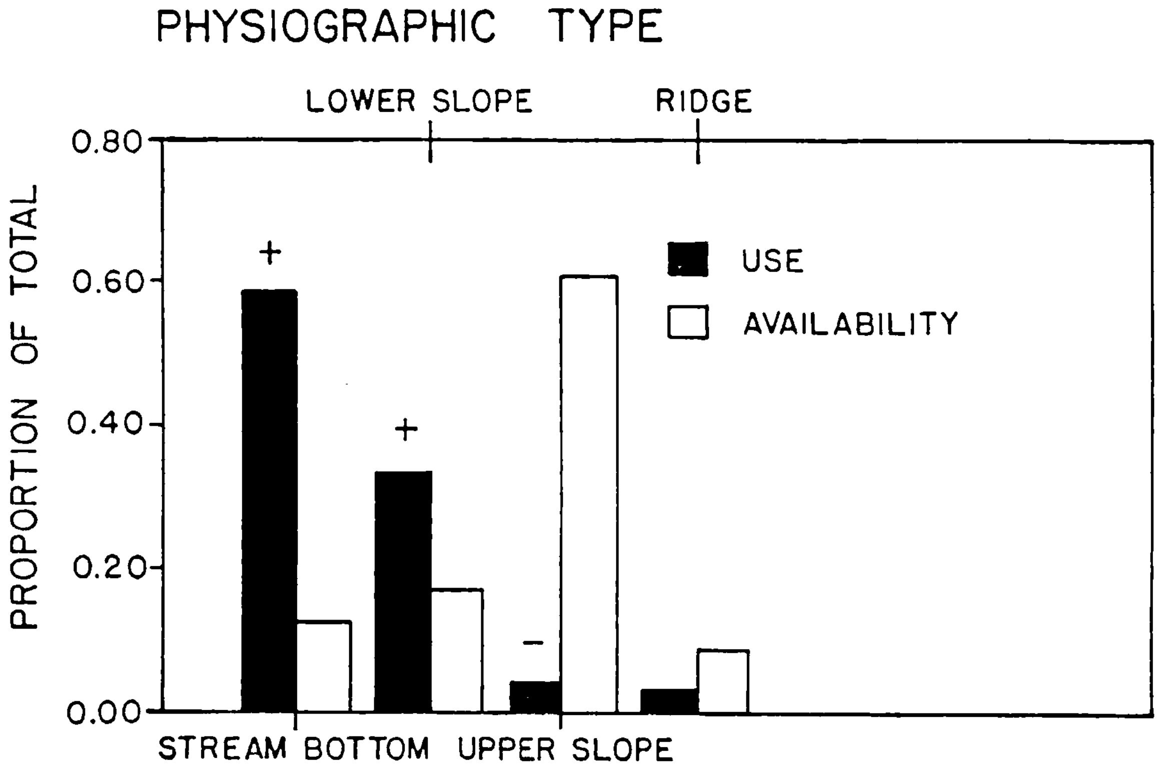

Fig. 4. Proportionate use of physiographic types for feeding sites by Sumatran rhinos compared with their availability in the study area as determined by 100 random points (X^2=186, df=3, P<0.001). A + or - indicates use significantly different than the availability of the habitat category (P<0.1).

m) was significantly lower than the mean elevation of the study area (542 m) (t=8.0, df=417, P<0.001; Fig. 5). Likewise, the rhinos selected feeding sites with a mean slope (8.3%) less than the mean (17.3%) of the study area (t=7.2, df=587, P<0.001; Fig. 6). The distance between feeding sites and the nearest stream with a permanent flow was 143 m.

Rhino selection of the canopy cover habitat attribute at feeding sites was apparent but more difficult to interpret. The mean percent canopy cover at feeding sites (83%) was significantly less than the mean for the study area (93%) (t=9.2, df=578, P<0.001; Fig. 7). In terms of successional stage, the rhinos showed a significant positive selection for the old gap category (Fig. 8). Likewise, the use of the closed canopy forest (63%) was less than its availability in the study area (83%). No significant difference was found between use and availability of the new gap and riverine types. By collapsing the number of successional stage categories into gap and non-gap sites, the dimensionality of the problem was reduced. The rhinos fed in forest gaps 35% of the time, significantly higher than their availability (15%). Also, 44.6% of the total number of rhino bites were at feeding sites located in forest gaps, although the mean number of bites per plant was not significantly higher (P=0.30). These rhinos used small forests gaps for feeding more than their availability, indicating a selection for small open areas. On the other hand, a majority of the feeding cases (63%) was in the closed canopy forest. Although the rhinos showed a selection for small forest gaps for feeding sites, the closed canopy forest was still an important habitat for feeding.

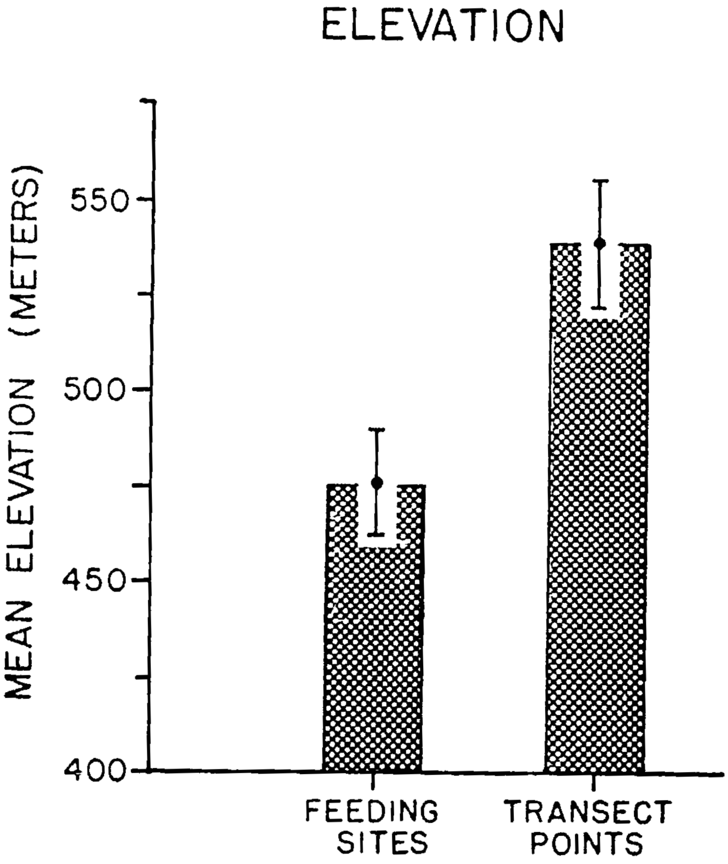

Fig. 5. Mean elevation of Sumatran rhino feeding sites ($\bar{x}$=478 m, SD=71, n=319) compared with the mean elevation of the study area as determined by random points ($\bar{x}$=542, SD=67, n=100). Each mean is bounded by a 95% confidence interval.

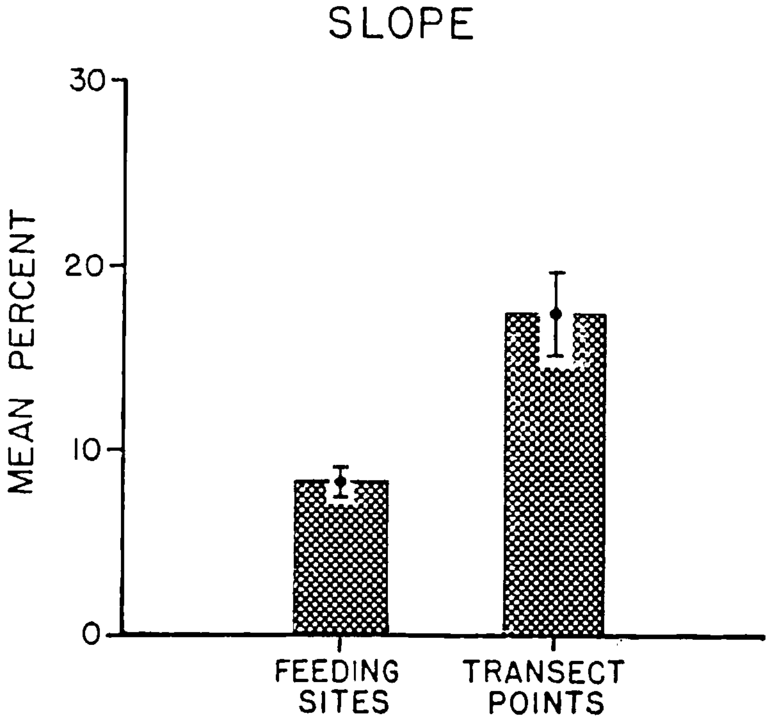

Fig. 6. Mean percent slope of Sumatran rhino feeding sites ($\bar{x}$=8.3, SD=10, n=309) compared with the mean slope of the study area ($\bar{x}$=17.3, SD=17, n=280). Each mean is bounded by a 95% confidence interval.

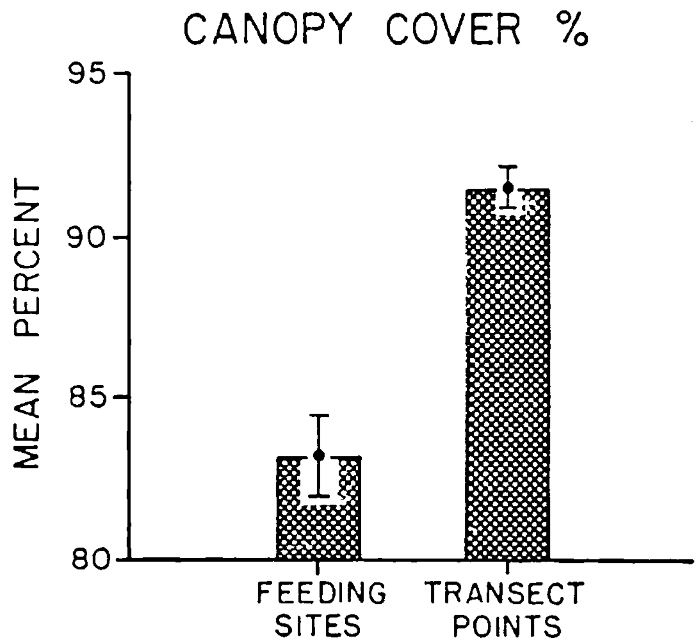

Fig. 7. Mean percent canopy cover of Sumatran rhino feeding sites ($\bar{x}$=83, SD=16, n=300) compared with the mean percent canopy cover of the study area ($\bar{x}$=93, SD=9, n=280). Each mean is bounded by a 95% confidence interval.

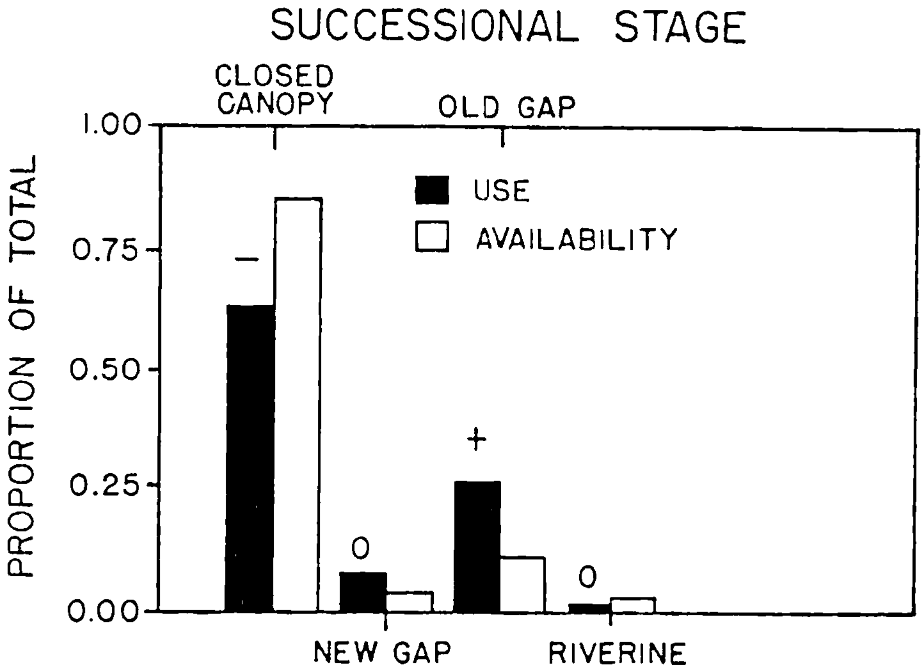

Fig. 8. Proportionate use of successional stages for feeding sites by Sumatran rhinos compared with their availability in the study area as determined by 280 transect points ($X^2=30$, df=3, $P<0.001$). A + or - indicates use significantly different than the availability of that habitat category ($P<0.1$).

Diet Composition

Plant life form. Woody saplings were the dominant plant life form type (95.6%) selected for feeding (Fig. 9). Woody saplings consisted of shrubs, small understory trees, and juveniles of mid-canopy and large emergent trees. Woody climbers (vines) were the next most frequently eaten plant form (3.5%). Often these climbers were growing on saplings that were consumed by the rhinos. Some feeding on climbers appeared almost incidental to eating the saplings. Only 2 palms and 1 herbaceous plant were consumed, and in each case little foliage was removed.

Rhinos selected plants within a narrow range of stem diameters for feeding. The stem diameter at breast height (DBH) varied from 0.4 to 6.0 cm ($\bar{x}$=1.9 cm, SD=1.1, n=317); about 68% of the plants had stem diameters between 0.8 and 3.3 cm. Woody saplings with large stem diameters were seldom selected for feeding because the stems were probably difficult to push or break. The height of food plants was more variable and had less influence on food selection ($\bar{x}$=3.3 m, SD=1.8, n=301). Usually, stems taller than 1.5 m were broken or pushed to the ground so the leaves would be available for feeding.

Botanical composition. During the study, 11,818 rhino bites on 342 individual plants were recorded. The food plants consisted of 49 families, 102 genera, and from 156 to 181 species. Identification of food plants proved to be a difficult problem. Because plants could not be identified in the field, a leaf sample was collected from each plant for later identification by forest botanists. These botanists had

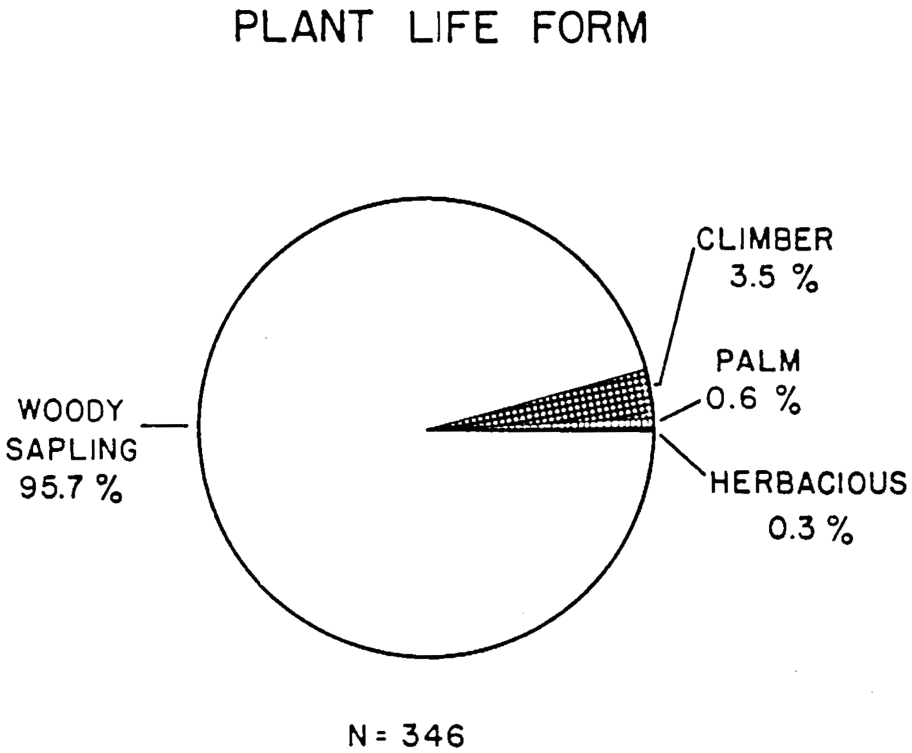

Fig. 9. Proportion of plant life forms in Sumatran rhino diets.

difficulties in identifying the plants to species because only sterile samples were available from my collections, little plant collecting has been done in the Endau-Rompin region, and the taxonomy of many understory plants, especially the Rubiaceae, was poorly known. Thus, only about 70% of the plant samples were identified to species, but most of them were classified to genus. The food plant list contained several new records for the region and possibly 2 new species (K. Kochummen, pers. comm.). Because of the lack of species names for many of the plants, I grouped the plants by family or genus for many of the analyses.

The great diversity in the tropical forest understory presented many problems in the interpretation of diet composition and food selection. The botanical composition of rhino diets reflected the species diversity of the habitat. About 46% of the feeding cases were different species. Even at the generic level, diversity in the diet was high with 102 genera represented in the 342 cases of feeding. The food plant list contained 46% of the total number of woody plant families occurring in Peninsular Malaysia.

The relationship between the cumulative number of plant genera in the food plant list and the cumulative number of feeding cases was studied to determine the number of feeding cases needed to accurately sample diet composition at the generic level (Fig. 10). The first 100 feeding cases consisted of 55 different plant genera. This curve leveled off at about 250 feeding cases; the last 100 cases added only 6 new plant genera, the rest being replicates. This information indicated

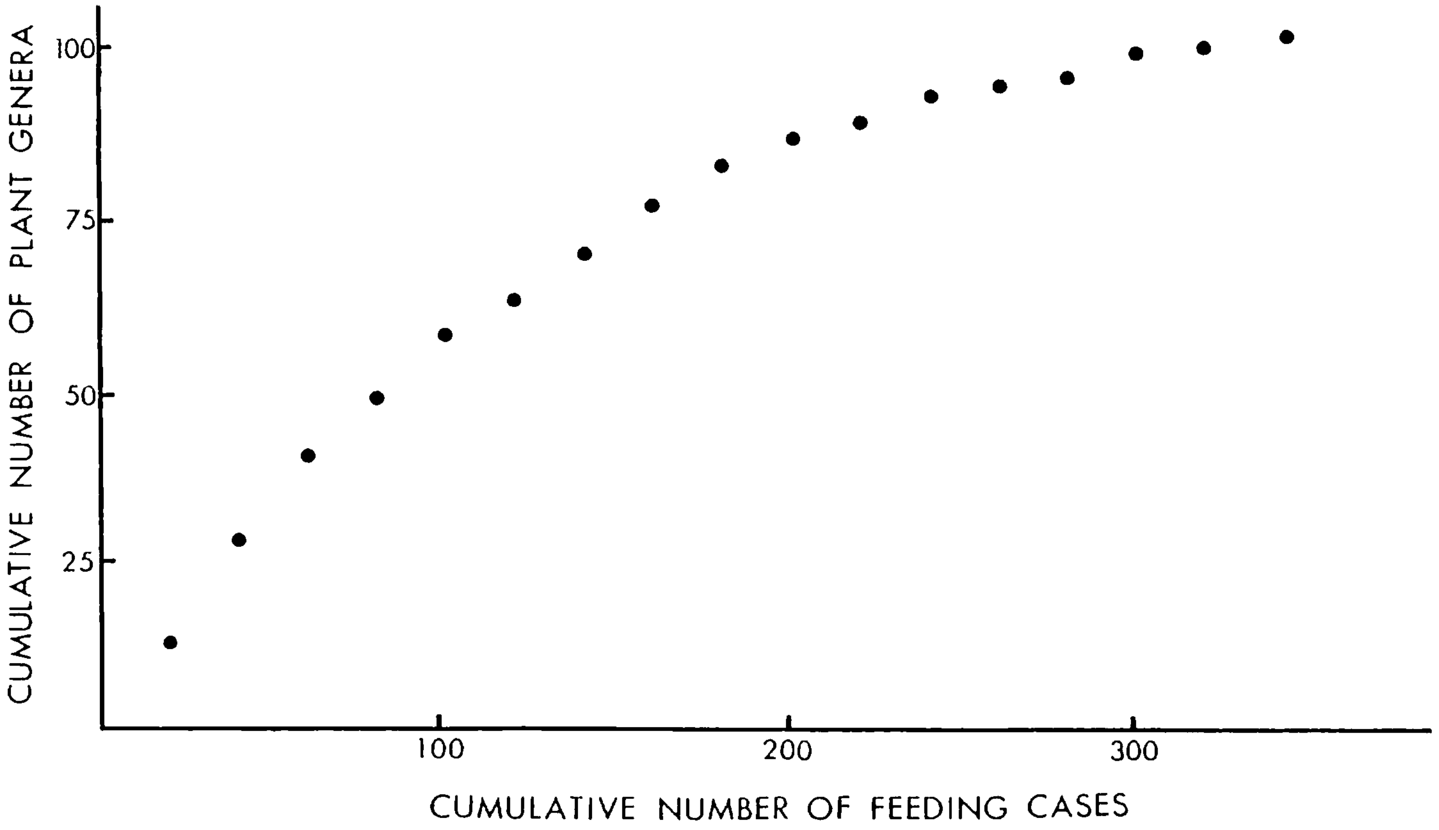

Fig. 10. Relationship between the cumulative number of Sumatran rhino feeding cases examined and the cumulative number of plant genera recorded. In 342 feeding cases, 102 plant genera were identified.

that a sufficient number of feeding cases had been observed to accurately describe diet composition at the generic level.

Composition of Sumatran rhino diets was estimated by dividing the cumulative number of bites per plant taxon by the total number of bites recorded during this study. The data collected during all time periods were pooled for this analysis because no differences between years or seasons were observed. Diet composition was evaluated by plant family (Table 1) and plant genus (Table 2). At the family level, principal food plants contained 27 of the 49 families on the food plant list, 92% of the total bites, and 89% of the total feeding cases. Plant families Rosaceae and Rubiaceae contributed the largest number of bites to the rhino´s diet, collectively about 30%. Moraceae, Meliaceae, Euphorbiaceae, Icacinaceae, and Celastraceae were the next most important families in the diet, each contributing more than 4%. The rest of the principal plant families composed from 1 to 3% of the diet. The remaining 22 plant families contributed only 8% of the total rhino bites, or an average of 0.36% of the diet each.

Evaluated at the generic level, 30 of the 102 plant genera in the food plant list contributed 1% or more of the total number of bites. These principal genera of food plants contained 74% of the total number of bites and 64% of the feeding cases. _Prunus_ was the most frequently eaten plant genus and contributed the largest number of bites (15.1%) to the diet, more than twice the amount of _Ficus_ (6.4%). Together with _Pavetta_ (6.1%), _Medusanthera_ (3.8%), and _Eugenia_ (3.0%), these plant genera composed 35% of the rhino´s diet; they appeared to be the key

Table 1. Principal plants in the diet of the Sumatran rhinoceros in the Endau-Rompin region, feeding cases grouped by plant family. Plant taxa ranked by percentage of total number of bites recorded during the study period.

Plant family[a]	Rank	Percentage of diet[b]	Number of feeding cases[c]	Number of bites/plant[d]
Rosaceae	1	15.0	46	38
Rubiaceae	2	14.7	47	36
Moraceae	3	8.1	24	40
Meliaceae	4	5.5	15	43
Euphorbiaceae	5	5.1	27	22
Icacinaceae	6	4.1	13	37
Celastraceae	7	4.0	7	66
Myrsinaceae	8	3.3	12	32
Leguminosae	9	3.1	6	61
Sapotaceae	10	3.0	9	39
Myrtaceae	11	3.0	12	29
Theaceae	12	2.3	4	67
Lauraceae	13	2.2	12	21
Ulmaceae	14	2.2	2	127
Myristicaceae	15	1.8	5	43
Flacourtiaceae	16	1.5	4	43
Actinidiaceae	17	1.4	3	55
Sapindaceae	18	1.4	8	20
Guttifera	19	1.3	5	31
Rutaceae	20	1.3	5	30
Verbenaceae	21	1.3	8	19
Oleaceae	22	1.2	6	22
Aceraceae	23	1.1	2	67
Rhizophoraceae	24	1.1	5	26
Ebenaceae	25	1.1	6	22
Dipterocarpaceae	26	1.0	6	18
Loganiaceae	27	1.0	2	52
TOTALS		92.0	301	41

[a] Plant families contributing more than 1% of the total number of bites.

[b] Total number of bites = 11,818.

[c] Total number of feeding cases = 342.

[d] Mean number of bites per plant.

Table 2. Principal plants in the diet of the Sumatran rhinoceros in the Endau-Rompin region, feeding cases grouped by plant genus. Plant taxa ranked by percentage of total bites.

Plant genus[a]	Rank	Percentage of total bites[b]	Number of feeding cases[c]	Mean no. of bites/plant
Prunus	1	15.1	46	38
Ficus	2	6.4	19	39
Pavetta	3	6.1	16	44
Medusanthera	4	3.8	11	40
Eugenia	5	3.0	12	29
Pithecellobium	6	2.9	5	69
Lasianthus	7	2.7	7	44
Bhesa	8	2.3	4	67
Palaquium	9	2.2	6	43
Aglaia	10	2.2	9	28
Gironniera	11	2.1	2	127
Adinandra	12	1.9	3	75
Ardisia	13	1.9	7	32
Chisocheton	14	1.7	1	200
Artocarpus	15	1.6	4	45
Macaranga	16	1.5	9	19
Urophyllum	17	1.5	9	19
Saurauia	18	1.4	3	55
Glyptopetalum	19	1.4	2	82
Maesa	20	1.4	5	32
Gardenia	21	1.4	4	39
Randia	22	1.3	7	21
Litsea	23	1.3	7	21
Chionanthus	24	1.2	6	22
Acer	25	1.1	2	67
Diospyros	26	1.1	6	22
Garcinia	27	1.1	4	31
Gymnacranthera	28	1.1	3	41
Dysoxylum	29	1.0	4	29
Antidesma	30	1.0	4	28
TOTALS		74.6	216	48

[a] Plant genera contributing 1% or more of the total number of bites.
[b] Total number of bites = 11,818.
[c] Total number of feeding cases = 342.

forage group. Most of the plant genera were poorly represented in the diet; 50 genera were recorded only once. The lowest 72 genera in the diet contributed an average of 0.35% to the diet. Individuals of these plant genera may have been uncommon in the habitat or highly unpalatable.

The mean number of bites per plant was quite variable, but illustrated whether many small plants or a few large plants contributed to the diet proportions. Because of the problem with differences in plant size, diet proportions based on the relative frequency of stems gave a different estimate of diet composition than total bites.

Diet composition was not evaluated at the species level because of the problems mentioned previously. _Prunus arborea_, _Pavetta indica_, and _Medusanthera gracilis_ contributed the largest diet proportions at the species level. Each of these species were single members of a genus that were eaten frequently. Most of the plants at the species level contributed only 1 or 2 feeding cases and a small proportion of the total number of bites.

Plant parts. Mature leaves accounted for 85.5% of the total bites at feeding sites. Stem material (8.6%) and young leaves (1.4%) were eaten in much smaller proportions. The use of young leaves was difficult to assess because young leaves were a small proportion of the available leaves on a plant (less than 2%), and they may have been eaten completely. Thus, the proportion of young leaves in the diet may have been slightly underestimated. Young leaves, mature leaves, and stem material were often eaten together at the same plant, often in about the same proportion as their availability. Mature leaves were the most available plant part (82%) at all sites. Much of the stem material consumed appeared to have been incidental to eating mature leaves. Young and mature leaves were always used more than stem material. Stems larger than 5 mm in diameter were seldom eaten.

The proportion of fruit in the diet was difficult to determine, so I treated fruits separately from the other plant parts. Rhino tracks were followed to fruiting trees 15 times, and the animals appeared to eat fallen fruit from the ground. I was unable to quantify the number or amount of fruit eaten. The importance of fruit in the diet was estimated by examining 65 dung piles for seeds. The frequency of occurrence of fruit seeds in the dung was assumed to be reflective of the amount of fruit eaten. Fruit seeds were found in 10 (15%) of the dung samples. The rest of the dung material was usually leaf or stem matter from woody saplings. Fruit consumption was quite seasonal with most use recorded from March to September, the main fruiting period for many forest trees. All large, fleshy fruits appeared to be highly preferred food items, especially wild mangos (_Mangifera_ sp.)(Table 3). The identification of fruits and seeds was difficult because many of them had not been collected previously. When a large tree was fruiting heavily, rhino trails often returned to the same tree several times. During April 1981, several mango trees were fruiting at the same time near the Selai base camp, and fresh rhino tracks were found at these trees daily. While following tracks at other times, the rhinos occasionally returned to trees where they had eaten fruits previously.

Table 3. Forest fruits recorded as eaten by Sumatran rhinos in the Endau-Rompin region. Information collected from the observation of feeding evidence or of seeds in dung samples.

Family	Species
Anacardiaceae	*Mangifera foetida*
Anacardiaceae	*M. lagenifera*
Anacardiaceae	*M. microphylla*
Guttiferae	*Calophyllum macrocarpum*
Leguminosae	*Parkia* sp.
Rhizophoraceae	*Anisophyllea griffithii*
Rosaceae	*Parinari* sp.
Rutaceae	*Citrus* sp.

Forest fruits are probably an important source of nutrients and highly palatable. The rhinos, in turn, probably function as important seed-dispersing agents for the seeds of some trees. Mango seedlings were found sprouting in rhino dung on 5 occasions.

Use Index

The percentage of leaf and stem matter eaten from each plant at feeding sites was recorded as a use index. For all feeding cases, this index ranged from 0 to 100 ($\bar{x}$=44, n=342). Plant genera with a mean index greater than 44 have been listed in Table 4. Many of the plant genera with high use values contributed little to diet proportions. Plants with high use indices were probably quite rare in the habitat. Principal food plants were often used less on an individual basis with use indices clumped around the mean. On the other hand, some plants with a low use index were eaten infrequently, suggesting that they were unpalatable.

Ecological Characteristics of Food Plants

The ecological characteristics of rhino food plants were investigated by reviewing the available information on the groups, primarily that by Symington (1933), Van Steenis (1953), Burkill (1966), Whitmore (1972), Wyatt-Smith and Kochummen (1979), and Kochummen (pers. comm.). In regard to canopy position, 75% of the feeding cases were plants typical of the forest understory (Fig. 11). In contrast, 18% of the feeding cases were juvenile trees that usually reach the mid-canopy position at maturity. Only 2.8% of the feeding cases were

Table 4. Use index of plants eaten by Sumatran rhinos in the Endau-Rompin region, cases grouped by plant genus.

Plant Genus[a]	Rank	N	Use index[b]
Chisocheton	1	1	76.9
Styrax	2	1	74.6
Clerodendrum	3	2	74.5
Tetractomia	4	1	72.5
Saurania	5	2	72.4
Dysoxylum	6	3	68.7
Anisophyllea	7	1	66.9
Baccaurea	8	1	65.1
Aglaia	9	5	62.3
Lophopetalum	10	1	60.4
Lasianthus	11	5	59.8
Gardinia	12	3	59.1
Erycube	13	1	58.9
Cynometra	14	1	57.1
Melastoma	15	1	57.1
Artocarpus	16	4	57.0
Pimeleodendron	17	1	56.7
Aphanamiris	18	1	56.5
Acronychia	19	1	55.5
Amaracarpus	20	2	54.4
Macaranga	21	6	54.1
Bhesia	22	4	53.4
Acer	23	2	52.6
Nothophoebe	24	1	52.4
Palaquim	25	5	52.3
Garcinia	26	3	51.5
Pavetta	27	16	51.5
Aporusa	28	6	50.5
Quercus	29	3	49.5
Ardisia	30	5	49.2
Pithecellobium	31	4	48.7
Tinomiscium	32	2	46.4
Adinandra	33	3	46.0
Prunus	34	36	46.0
Medusanthera	35	10	45.1
TOTAL		144	55.5

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[a] Plant genera with a mean use index greater than 45.

[b] Mean.

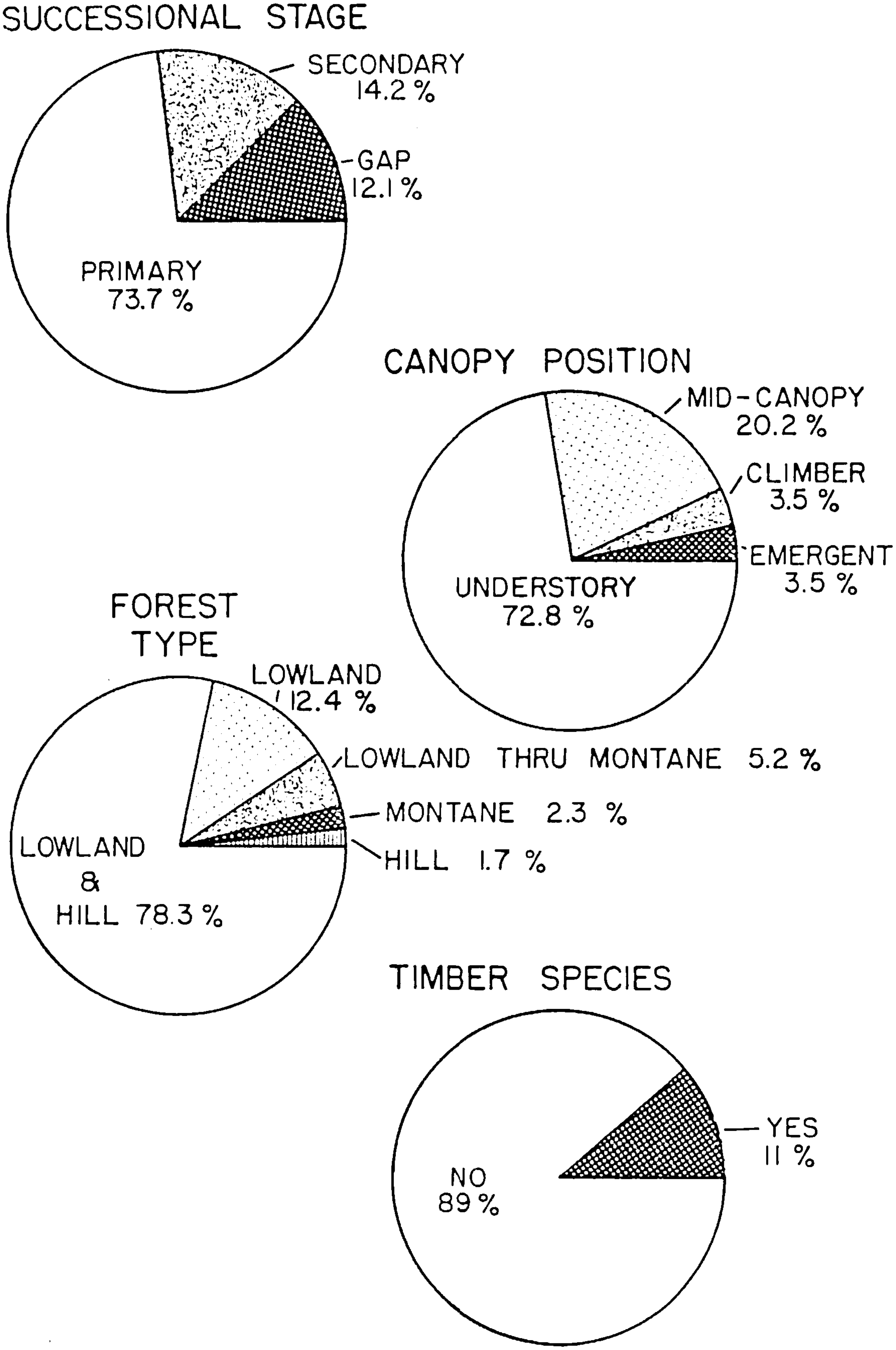

Fig 11. Ecological characteristics of plants eaten by Sumatran rhinos.

juveniles of emergent trees. Likewise, only 10% of the feeding cases were juveniles of timber trees.

In terms of successional stage, 74% of the plants were characteristic of the primary closed canopy forest. Only 14% of the feeding cases were plants typical of secondary vegetation and 11% were of forest gaps. Most of the food plants were trees typically found in lowland and hill forest (78%). A smaller number were commonly restricted to lowland forest (12.5%) or montane forest (2.5%). A few had wide ecological distributions, ranging from lowland through montane forest (4.7%).

Food Availability

The availability of potential food for feeding rhinos in the forest understory was estimated from the enumeration of saplings within the rhino food size class along transects (Table 5). The mean density of woody saplings between 0.8 and 3.2 cm DBH was found to be significantly different among the physiographic types (ANOVA, f=4.5, P=0.004), varying from 4710 stems/ha on the ridges to 6740 stems/ha in the stream bottom type. Woody sapling densities in the lower and upper slope types were intermediate at 5000 and 4990 stems/ha. Likewise, the stream bottom type had the largest amount of availble leaf matter (550 kg/ha) and the ridge type had the least amount (310 kg/ha). These data indicated that the largest amount of potential food for foraging rhinos was available in the stream bottom type and the quantity of available food decreased with increasingly steep topography.

Several of the enumerated saplings were identified to genus

Table 5. Density of woody saplings (0.8 to 3.2 cm DBH) in the forest understory, by physiographic type. Data collected from the enumeration of 1120 saplings at 280 points along 14 transects. Amount of available biomass was calculated by multiplying total number of bites of mature leaf per plant times the mean weight of 1 standard bite (2.4 g).

Physiographic type	N	Sapling density stems/ha		Leaf biomass kg/ha
		$\bar{x}$	SE	
Stream Bottom	320	6740	380	550
Lower Slope	320	5000	300	370
Upper Slope	320	4990	320	360
Ridge	160	4710	430	310
All sites	1120	5370	190	390

and provided information on the relative density of certain food plants (Table 6). *Eugenia* sp. was the most frequent woody sapling in the forest understory, comprising about 6% of the stems within the rhino food size class. *Shorea* sp., a non-principal food plant, and *Pavetta* sp., a highly used food plant, were the next most common taxa of plants in the understory (about 4.5% each). *Quercus* sp. and *Xerospermum* sp., seldom used plants, each comprised about 3% of the understory. *Prunus* sp., the most highly used plant, comprised about 1% of the stems in the understory. Because of the high diversity of the understory, the remainder of the food plants probably composed less than 1% of the stand. Generally, rhino food plants occurred at low relative densities in the forest understory, most comprising less than 1% of the stand. Under the classic definition of preferred plants, use greater than availability (Petrides, 1975), most of the food plants could be considered as preferred food because diet proprortions were greater than their relative densities in the habitat. In tropical rain forest habitats, this type of analysis was not meaningful.

Several important food plants were found more frequently in the stream bottom and lower slope physiographic types. In the stream bottom type, the stand consisted of 2.1% *Prunus* sp. and 10% *Eugenia* sp. In the ridge type, the proportion of *Prunus* in the understory dropped to 0.0% and *Eugenia* to 3.8%. This trend was consistent for all food plants enumerated, indicating that the availability of food plants was higher in the stream bottom type, and they decreased in abundance with increasing elevation. A similar trend was observed in total sapling

Table 6. Relative abundance of certain plant taxa (0.8 to 3.2 cm DBH) in the forest understory. Information collected from the enumeration of 1120 saplings at 280 points along 14 transects during March through May 1981. Data grouped by physiographic type, expressed as the percentage of saplings in that category.

Taxa	Physiographic type				
	Stream bottom	Lower slope	Upper slope	Ridge	All types
Prunus sp.	2.1	2.2	0.3	0.0	1.1
Pavetta sp. [a]	4.0	3.1	6.3	3.2	4.3
Eugenia sp.	10.0	5.9	4.4	3.8	6.3
Garcinia sp.	1.3	0.6	1.3	3.2	1.3
Quercus sp. [b]	4.7	1.9	3.1	1.3	3.0
Pithecelobium sp. [c]	0.0	1.3	1.9	0.0	0.9
Xerospermum sp.	3.1	2.2	4.1	1.3	3.2
Shorea sp.	5.3	3.2	5.3	3.2	4.4

[a] Probably includes other members of Family RUBIACEAE.

[b] Includes Lithocarpus.

[c] Probably includes other members of Family LEGUMINOSAE.

density.

Understory Phenology

The phenology of woody saplings in the forest understory was studied by recording the proportion of young and mature leaves on saplings enumerated along transects (Table 7). Most of the leaf material in the forest understory consisted of mature leaves. Only about 11% of the saplings had young leaves present. Based on the total number of bites present on enumerated saplings, young leaves comprised only about 1.7% of the leaf material. The mean number of bites of young leaves per plant was 0.57, or 1.4 g of leaf matter, compared with an average of 29.3 bites (70 g) of mature leaf. In regards to physiographic type, woody saplings in the stream bottom and lower slope types had a higher proportion of stems with young leaves present (0.14) than upper slope and ridge types (0.08). This same trend was reflected by the mean number of young leaves per stem and the mean percentage of young leaf per stem.

Plant Chemistry

Leaf and stem material from certain plants actually eaten by rhinos and a sample of mature leaf from non-food plants were analyzed for their chemical composition. Chemical assays of each type were not available for all samples, so sample sizes varied depending on assay. Information for all chemical assays, except magnesium, was available from 87 plants eaten by rhinos and 27 non-food plants collected along transects.

Table 7. Phenology of woody saplings in the forest understory (0.8 to 3.2 cm DBH), by physiographic type. Information collected from the enumeration of 1120 saplings at 280 points along 14 transects during March through May 1981.

Physiographic type	N	Proportion of stems with YL present		Bites YL/Stem		YL per stem %	
		$\hat{p}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Stream Bottom	320	0.12	0.02	0.57	0.11	1.42	0.25
Lower Slope	320	0.15	0.02	0.78	0.13	2.43	0.37
Upper Slope	320	0.08	0.02	0.37	0.09	1.32	0.33
Ridge	160	0.08	0.02	0.52	0.18	1.21	0.38
All sites	1120	0.11	0.01	0.57	0.06	1.65	0.17

YL = young leaf.

A principal components analysis of the food plant samples showed the intercorrelations of the plant chemistry variables. The first 2 principal components contained 54% of the variance of the data set. PC-1 was interpreted as illustrating the overall correlations of the plant chemistry variables (Fig. 12). ASH, P, N, Ca, and K were all positively correlated with PC-1; TP, CT, and ADF were negatively correlated. In PC-2, Ca and ASH were highly positively correlated and ADF negatively. The PC analysis indicated that if a rhino ate leaves high in crude protein content, the leaves would also contain high concentrations of most minerals and low amounts of fiber and tannins. In contrast, the intercorrelations of the plant chemistry variables in the non-food plants were different compared with the food plants. In the non-food plants, N and P were not correlated with ASH, Ca, and K in PC-1 (Fig. 13). Instead, P and N were positively correlated with PC-2. The relationships among ASH, Ca, K, TP, CT, and ADF remained similar to the food plants.

Diet quality. The nutritional quality of diets depended on the proportions of the various forages and the chemical composition of those forages. Diet quality was estimated by the sum of the forage chemical values times weighted diet percentages (Table 8). The rhino′s diet was characterized as high in fiber (45% ADF); moderate in some minerals(K, CA, and ASH), phenolic compounds (TP 4.0% and CT 6.8%), and crude protein (11.3%); but extremely low in phosphorus (0.077%). The low amount of P in the diet resulted in a high CA to P ratio (12:1). The large amount of fiber and phenolic compounds in the diet yielded a

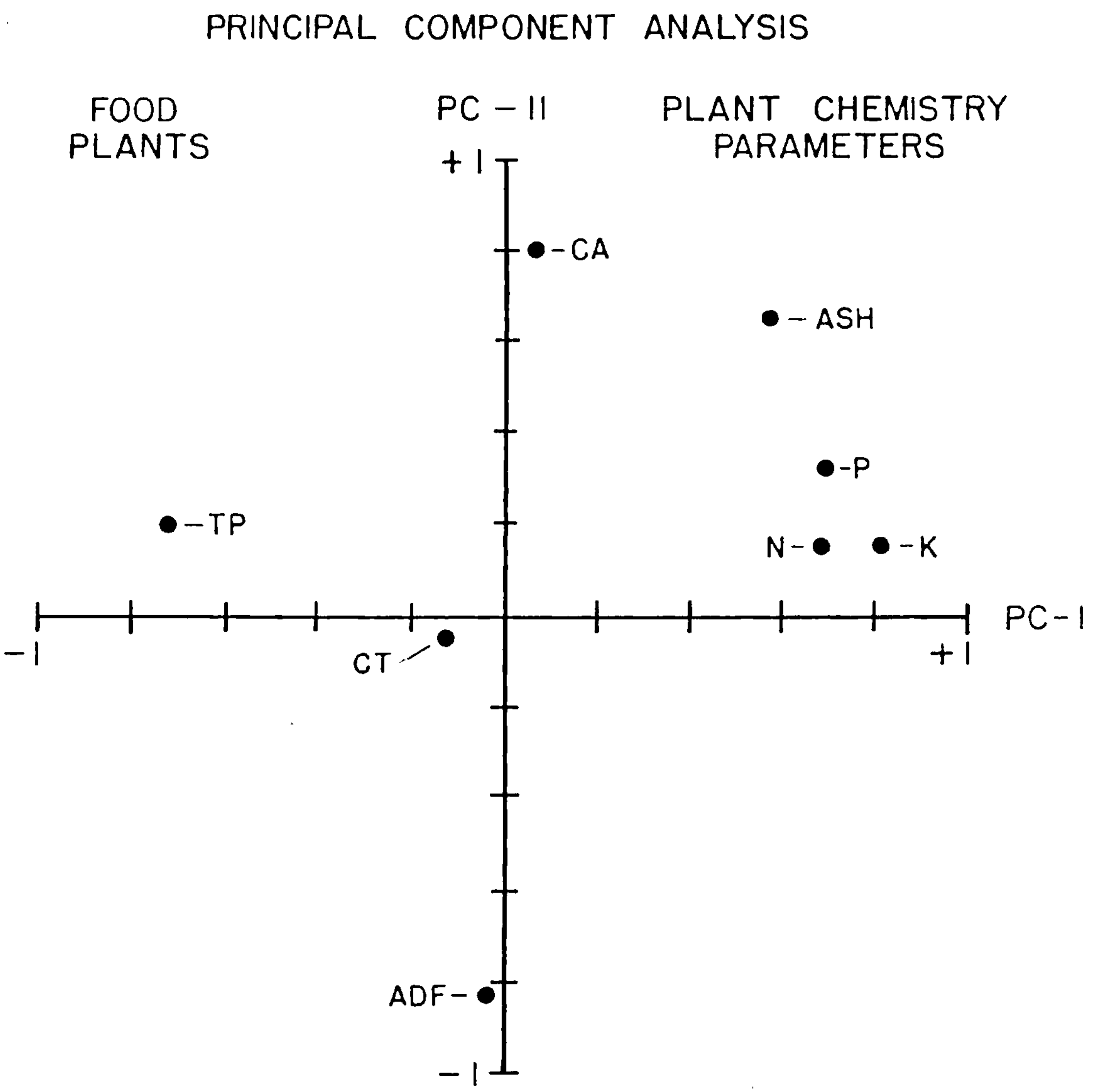

Fig. 12. Plant chemistry parameters of mature leaf material, collected from certain Sumatran rhino food plants, plotted on the first 2 principal components. PC-I and PC-II contained 54% of the variance in the data set. N = nitrogen, P = phosphorus, Ca = calcium, K = potassium, TP = total phenolics, CT = condensed tannins, ADF = acid detergent fiber.

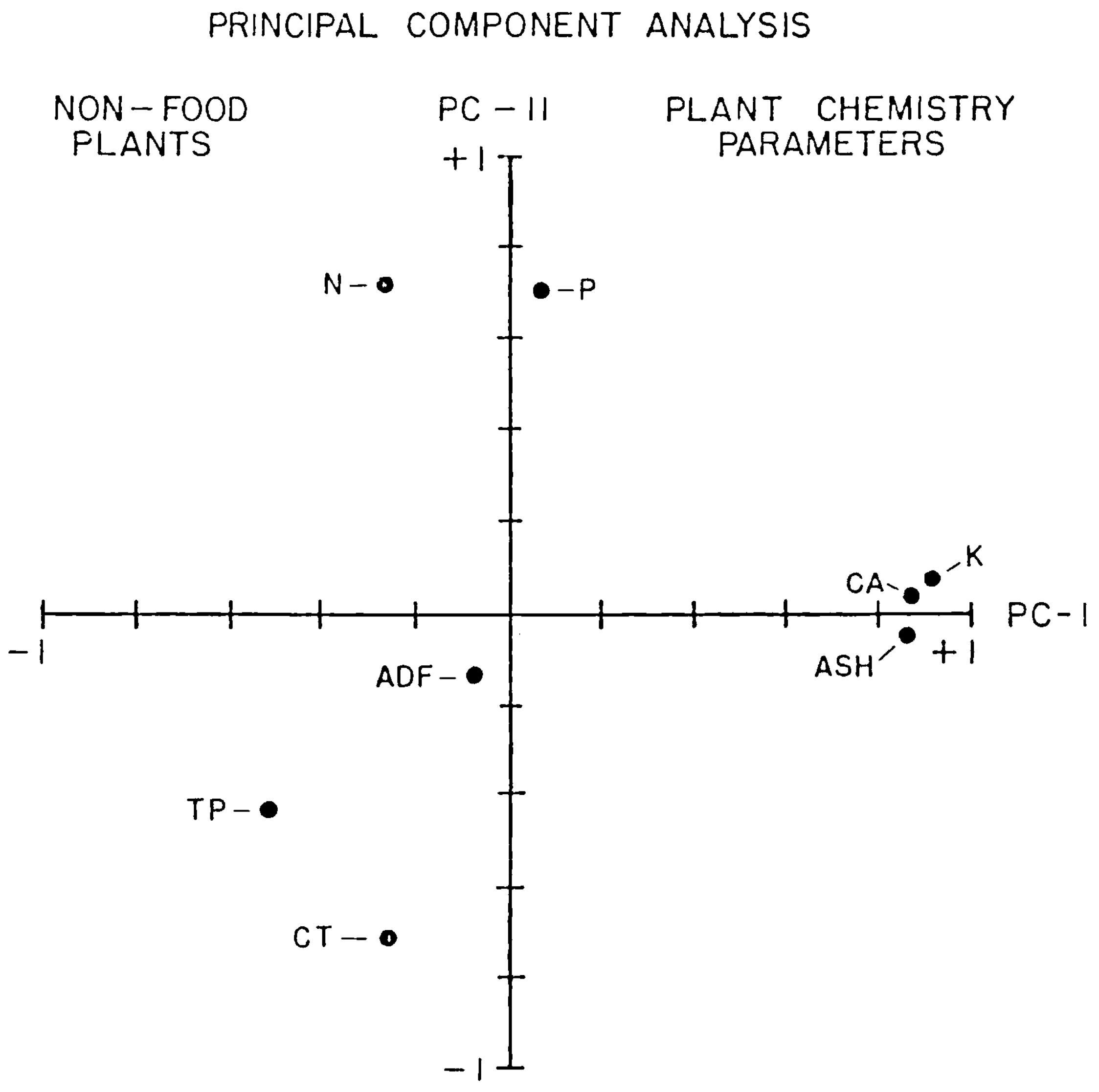

Fig. 13. Plant chemistry parameters of mature leaf material from certain non-food plants, selected randomly along transects, plotted on the first 2 principal components. PC-I and PC-II contained 56% of the variance of the data set. Key: see Fig. 12.

Table 8. Chemical composition of Sumatran rhino diets.

Assay	Diet composition
ASH (%)	6.68
N	1.80
P	0.077
Ca	0.86
K	1.08
TP	3.99
CT	6.83
ADF	44.77

Key: ASH = total ash, N = nitrogen, P = phosphorous, Ca = calcium, K = potassium, TP = total phenolics, CT = condensed tannins, ADF = acid detergent fiber.

crude protein to CT plus ADF ratio of 0.218.

According to a review of the available literature, plants eaten by Sumatran rhinos contained few plant toxins (Fig. 14). Of the plant genera with information available, only 3.3% of the feeding cases were plants known to contain alkaloids, a common plant toxin. About 21% of the feeding cases were plants known to contain saponins; 33% of the feeding cases were plant genera recorded as medicinal plants, indicating the presence of some kind of secondary plant compound. Of the 16 food plant samples actually screened (K. Chan, pers. comm.), only 2 mature leaf samples contained alkaloids and 3 samples contained saponins.

Plant parts. Pair-wise comparisons (Table 9) of mature leaf and stem matter collected from the same plants eaten by rhinos showed that mature leaves contained consistently higher dry-weight concentrations of Ash, N, P, Ca, K, and Mg, indicating a higher concentration of minerals and crude protein in mature leaves. Stem matter was higher in ADF than mature leaves for all samples. The concentration of CT was significantly higher in mature leaf material, but no difference was found in the content of TP. Generally, these data suggested that mature leaves were much higher in nutrient quality than stem material, except for the CT assay.

Rhino selection of plant parts for feeding reflected the nutrient composition of the parts. Excluding fruits, the diet consisted of 90% mature leaves and 8.6% stem material, showing a strong selection for mature leaves. For the most part, feeding on stem material may have been incidental to eating leaves. The lower amount of CT in the stems

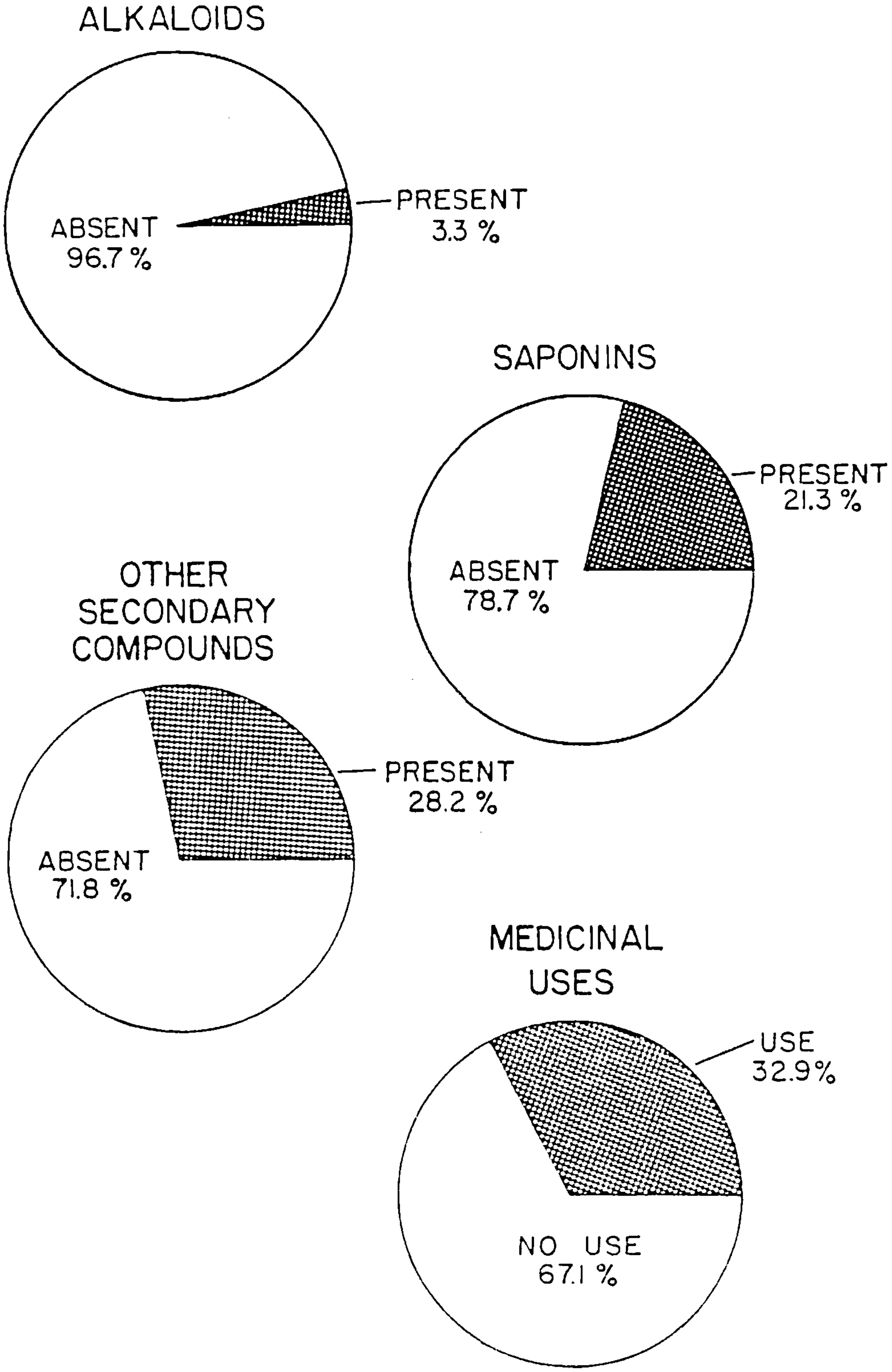

Fig. 14. Presence of certain secondary plant compounds in Sumatran rhino food plants. Information extracted from the literature, especially Burkill (1966), Carrick et al. (1968), Chan and Teo (1969), and Chan et al. (1972, 1977).

Table 9. Comparison of the chemical composition of mature leaf and stem material collected from plants eaten by Sumatran rhinos. All values are reported as percent dry matter.

Assay	N	Mature leaf		Stem		T[a]
		X	SE	X	SE	
Ash (%)	13	6.35	0.68	3.69	0.36	5.46***
N	13	1.57	0.18	0.78	0.08	5.86***
P	13	0.055	0.004	0.039	0.005	2.55*
Ca	13	0.79	0.13	0.55	0.11	4.85***
K	13	0.95	0.09	0.71	0.09	2.63*
Mg	12	0.35	0.03	0.15	0.02	6.03***
TP	10	5.07	1.41	2.53	0.48	2.13*
CT	10	6.51	2.19	6.64	1.91	-0.14
ADF	10	43.75	4.29	59.74	2.13	-4.23**

[a] Paired T-test, two-tailed probabilities.
*P<0.05; **P<0.01; ***P<0.001.
Key: see Table 8.

may have increased their palatability.

Unfortunately, little information was available for young leaves. Usually, the amount of young material available at a feeding site was too low for the chemical analyses. Only 1 sample of young leaf material was collected, Ardisia colorata. The young leaves of this plant were much higher in N, P, and K than mature leaves, but much lower than mature leaves in ADF and slightly lower in CT. The content of TP was slightly higher in the young leaves.

Food and non-food plants. The mature leaves of 68 plants eaten by rhinos were assayed for dry-weight composition of Ash, N, P, Ca, and K; 55 of the samples were additionally assayed for TP, CT, and ADF. Thus, complete information of the chemical composition of mature leaves was available for 55 taxa of food plants. In order to investigate whether the rhinos selected mature leaves for food based on their chemical composition, the food plant group was compared with a group of 25 non-food plants (Table 10). This comparison showed that the chemical composition of the food plant group was different than the non-food group. The food plant group contained significantly higher concentrations of Ash, N, P, and Ca, indicating that the animals selected plants higher in crude protein and mineral content. Although the groups were significantly different based on those chemical parameters, the absolute difference between the means was quite small for most assays. In contrast, the food plants were much lower in ADF, indicating a strong selection for plants low in fiber. The mean content of TP and CT was higher in the food plant group, although neither mean

Table 10. Comparison of the chemical composition of certain Sumatran rhino food plants collected at feeding sites and a sample of non-food plants collected at points along 3 transects. All values expressed as percent dry matter. For replicate samples of same species, the mean was computed before statistical tests were performed.

Assay	Food plants			Non-food plants			T^a
	N	X	SE	N	X	SE	
Ash (%)	68	6.85	0.35	25	5.67	0.45	1.87*
N	68	1.71	0.05	25	1.45	0.04	2.99**
P	68	0.069	0.002	25	0.057	0.003	2.63**
Ca	68	0.80	0.05	25	0.57	0.07	2.65**
K	68	1.12	0.07	25	1.02	0.08	0.99
TP	55	4.11	0.46	25	3.59	0.47	0.79
CT	55	6.33	1.04	25	3.45	0.72	1.79
ADF	55	45.82	1.32	25	56.32	1.92	-4.48***

[a] Two-sample T-test, two-tailed probabilities.

*$P<0.05$; **$P<0.01$; ***$P<0.001$.

Key: see Table 8.

was significantly different from the non-food group ($P<0.05$).

Principal food plants. Discriminant function (DF) analysis was used to investigate the ability to classify plant samples, based on their chemical composition, into groups determined by the importance of the plant genera in the diet. For this analysis, the plant samples were grouped as principal food plants (genera contributing more than 1.5% of the diet), non-principal food plants (genera contributing less than 1.5% of the diet), and non-food plants. With all 3 groups and all 8 variables in the analysis, 2 discriminant functions were derived that classified 64% of all the cases accurately. DF 1 contained most of the variance of the data set (88%) and was interpreted as measuring differences in the concentrations of ADF, CT, and N. DF 2 contained a small proportion of the variance (12%) and had less discriminanting power. This function was interpreted as measuring differences in ASH, CT, ADF, TP, Ca, P, and N. To illustrate intergroup differences, the group centroids were graphed in a two-dimensional space based on DF 1 and DF 2 (Fig. 15). The best separation among group centroids was between food and non-food groups, with the non-food space high in ADF and low in minerals, N, and CT. Separation between principal and non-principal food plants was poor. The group centroids for principal food plants lay in a chemical space characterized by high ASH, N, and TP. The non-principal food group centroid lay in a space high in CT and ADF. K had little discriminanting power in this analysis.

Use index. DF analysis was used to determine whether plant

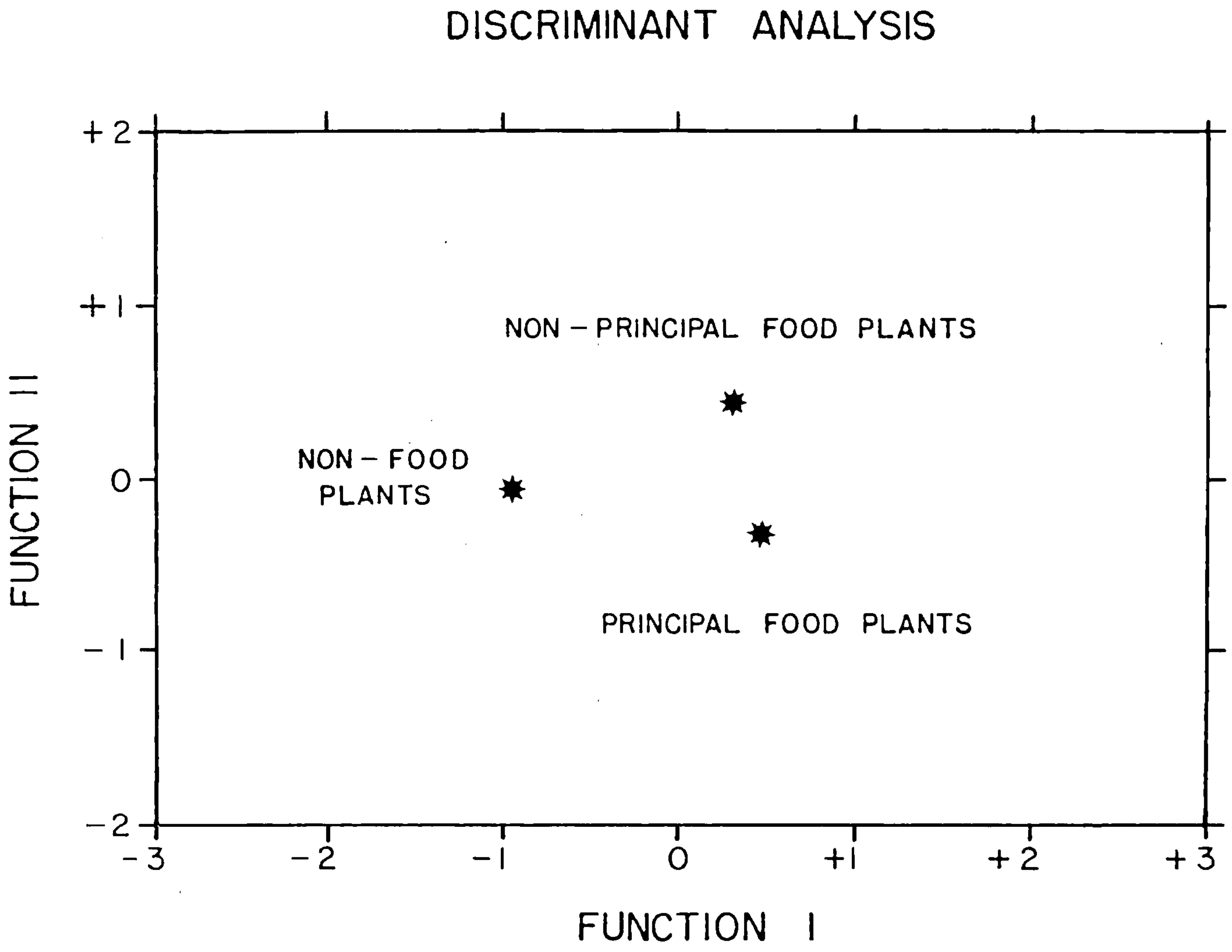

Fig. 15. Group centroids of plant samples plotted on 2 discriminant function axes based on plant chemistry variables. Mature leaf samples were grouped by principal Sumatran rhino food plants, non-principal food plants, and non-food plants. All plant chemistry variables (Ash, N, P, Ca, K, TP, CT, and ADF) were included in the analysis; 64% of the cases were classified correctly into their respective groups.

samples could be separated into use index groups based on their chemical composition. The feeding cases were put into 3 groups based on whether their use index was greater than the overall mean (44), less than the mean, or whether they were classified as non-food plants. With all 3 groups in the analysis, a significant discriminant function was derived (P=0.004) that properly classified 53% of the feeding cases into their respective groups. In this analysis, ADF and CT were the most useful discriminating variables. DF 1 contained most of the data set´s variance (90%); this function was interpreted as measuring differences in the concentrations of P, CA, and ADF. The best separation among group centroids was between food and non-food groups. The chemical space occuppied by non-food plants was high in ADF, and the food plants were high in P, CA, and CT. DF 2 had less discriminating power, essentially separating the food plants grouped by high and low use indices. The group centroid of the high use index plans lay in a chemical space high in ASH. P, and K. The group centroid of the low use index plants lay in a space high in N, CT, and ADF.

Crude protein/digestion inhibitor ratio. Rhino food plants were ranked based on the ratio of crude protein (N x 6.25) content to CT + ADF (Table 11). This ratio (CP/DI) has been found to be a good measure of forage quality, and is highly correlated with food selection in some species of primates (McKey et al., 1981). In the rhino food plants, this ratio ranged from 0.581 to 0.075 for 68 species. Many of the plants that were principal food plants, or had high use indices, also had a high CP/DI ratio. The rhino food plant group had a

Table 11. Calculated nutrient/digestion-inhibitor ratios for mature leaves of plants eaten by Sumatran rhinos.

Plant taxa	6.25 N/ (CT+ADF)	Percentage of diet	Use index[a]
Fagraea racemosa	0.581	<1.0	19
Pavetta indica	0.539	6.1	62
Medusanthera gracilis	0.529	3.8	44
Aglaia griffithii	0.419	2.2	65
Croton laevifolius	0.337	<1.0	17
Aphanamixis rohituka	0.335	<1.0	57
Ardisia oxyphylla	0.315	1.9	38
Lasianthus sp.	0.313	2.7	47
Ficus uniglandulosa	0.275	6.4	45
Antidesma cuspidatum	0.265	1.0	33
Gironniera nervosa	0.262	2.1	28
Diospyros sp.	0.252	1.1	--
Macaranga triloba	0.249	1.5	40
Bhesa paniculata	0.244	2.3	56
Khema curtisii	0.236	<1.0	36
Acer laurinum	0.232	1.1	52
Antidesma sp.	0.230	1.1	--
Eugenia densiflora	0.226	3.0	39
Macaranga pruinosa	0.220	1.5	87
Shorea leprosula	0.221	<1.0	44
Pimelodendron griffithianum	0.219	<1.0	57
Garcinia forbesii	0.218	1.1	9
Chionanthus oliganthus	0.217	1.2	47
Ficus chartaeae	0.216	6.4	33
Streblus elongatus	0.216	<1.0	44
Arytera sp.	0.212	<1.0	46
Glochidion sp.	0.207	<1.0	--
Timonius sp.	0.204	<1.0	7
Mischocarpus sp.	0.202	<1.0	43

[a] mean.

Key: See Table 8.

significantly higher CP/DI ratio than the non-food group (Mann-Whitney, rank sum test, P<0.001).

DISCUSSION

Sumatran rhinos in the Endau-Rompin study area use the understory vegetation of mature tropical rain forest for their food source. Few other mammals attempt this foraging strategy. Indirect information indicates that the understory of tropical rain forests is a poor habitat for mammilian herbivores. Mature rain forests of both the New world and the Old World tropics have a less diverse and less dense terrestrial ungulate fauna than savanna or grassland habitats (Eisenberg and McKay, 1974). In southern Asia, the biomass of terrestrial herbivores declines as forest cover becomes continuous (Eisenberg and Seidensticker, 1976). Within a mature tropical rain forest, arboreal herbivores typically constitute a majority of the mammalian biomass (Eisenberg and Thorington, 1973).

The once sympatric Javan rhino (Rhinoceros sondicus) is the only other extant rhinoceros that occupies rain forest habitats (Groves, 1967). Presently extinct in Malaysia (Medway, 1969), the Javan rhino predominantly uses lowland areas covered by riverine, swamp, or more disturbed forested habitats (Schenkel and Schenkel-Hulliger, 1969; Hoogerwerf, 1970). The African species, the black rhino (Diceros bicornis) and the white rhino (Ceratotherium simun), and the Indian rhino (Rhinoceros unicornis) occur in tropical or sub-tropical savanna or grassland habitats (Goddard, 1970; Owen-Smith, 1975; Laurie, 1982).

Of the 11 species of terrestrial mammalian herbivores found in Peninsular Malaysia (Medway, 1969), only 7 species occur in the mature hill forests of Endau-Rompin; none of them are abundant there (Flynn, unpubl. data). Most of these terrestrial herbivores prefer riverine areas or disturbed secondary forests for feeding habitats, especially elephants (Khan, 1977; Olivier, 1978), gaur (Weigum, 1972; Khan, 1973; Conry, 1981), wild pigs, and sambar deer (Medway, 1969). Only the Malayan tapir (Williams and Petrides, 1980), barking deer, and mouse deer frequent the mature hill forests that are also used by the rhinos (Medway, 1969).

Why is the understory of mature tropical rain forest a poor habitat for most mammalian herbivores? The understory is a unique habitat for plants. The overstory trees and vines form a nearly closed canopy, creating a microclimate characterized by constantly high humidity, relatively constant temperature, and low light intensity (Richards, 1952). Understory plants must be capable of establishing themselves and growing in the stable gloom of the high forest. In addition, tropical soils are generally nutrient poor, especially those susceptable to rapid leaching (Whitmore, 1975; Jordon and Herrera, 1981). The extensive root systems of overstory trees actively compete with the understory plants for available nutrients (Richards, 1952). Thus, understory species commonly persist for many years, but biomass and reproductive output is greatly reduced by competition with the forest canopy (Whitmore, 1975). Most understory plants are evergreen, and once leaves mature, they may remain for several years (Whitmore, 1975).

The slow growth rate and productivity of the mature rain forest understory were reflected by plant phenology. The vegetative transects indicated that few young leaves were present; 98% of the leaf biomass consisted of mature leaves, and only 11% of the stems had young leaves present. Few flowers or fruits were encountered. Janzen (1977) had similar observations. He hypothesized that the paucity of flowers and fruits on understory shrubs had a depressing effect on the biomass and species richness of the understory fauna. In contrast to the lowland forests of Costa Rica, Janzen (1977) concluded that the rain forests of Malaysia sit on a poor piece of real estate. Phenological studies of the overstory (McClure, 1966; Medway, 1972; Raemaekers et al., 1980) have recorded a much higher production of young leaves, flowers, and fruits. Some seasonality in leaf production existed; often young leaf production peaked during the same months (February to May) in which the vegetative transects were enumerated.

Each leaf in the understory represents a substantial investment in nutrients and energy by the plant; resources that are in short supply in the understory environment. In order to protect their investment, plants have evolved numerous defensive strategies to avoid leaf predators. Some plants, especially palms and climbers, are well protected by physical structures (i.e. thorns, spines, hairs, etc.) growing from their stems or leaves. Thorns and spines, particularly effective defenses against foraging terrestrial herbivores, probably evolved in response to browsing by mammals (Janzen, 1981). Of Malaysian mammalian herbivores, only elephants are capable of eating plants protected by thorns (Olivier, 1978).

Some plants escape herbivory by being unpredicatable in space and time (Feeny, 1976; Rhoades and Cates, 1976). The apparency of most understory plants in mature rain forests is greatly reduced by the high species diversity of the habitat. Over 4,000 species of woody plants occur in forests of Peninsular Malaysia (Whitmore, 1972); most of them are relatively rare and widely scattered in the understory (Whitmore, 1975). Aggregations of like individuals are seldom found, except in old fields, secondary forests, or forest gaps (Symington, 1933; Kochummen and Ng, 1977). In most ecological studies, stems smaller than 10cm DBH are rarely enumerated because of the vast number of species encountered (Poore, 1968; Whitmore, 1975) and the ephemeral nature of many juvenile trees (F. Ng, pers. comm.). In this study, Eugenia sp. was the most common genus of the understory plants, but comprised less than 6% of the stand. Most plant species probably contributed fewer than 1% of the understory stems.

Tropical rain forest plants use several chemical defensive strategies to avoid leaf predation (Rhoades and Cates, 1976). These plants contain a variety of secondary plant metabolites that influence food selection by mammalian herbivores (Freeland and Janzen, 1974; Rosenthal and Janzen, 1979). Tannins and alkaloids, two classes of secondary compounds that have received the most attention, are widespread in tropical vegetation (Burkill, 1966; Levin and York, 1978; McKey et al., 1978; Gartlan et al., 1980; Oates et al., 1980; Waterman et al., 1980; Becker, 1981). Generally, high concentrations of tannins, or other large phenolic compounds, reduce forage quality by interfering with animal metabolism, complexing with plant proteins, or inhibiting gut microfloras (Feeny, 1970; Freeland and Janzen, 1974; Rhoades and Cates, 1976; Becker, 1982). Mature leaves from woody plants collected in Endau-Rompin contained high concentrations of total phenolics ($\bar{x}$=3.9%, n=80) and condensed tannins ($\bar{x}$=5.4%, n=80). Phenolic compounds were absent from only 2 species. Compared with other rain forest sites, concentrations of condensed tannins in mature leaves from Endau-Rompin were similiar to those reported from tropical rain forest sites in Douala-Edea, Cameroon, (Gartlan et al., 1980) and Kakachi, India (Oates et al., 1980), but they were much higher than at Kibale, Uganda (Gartlan et al., 1980; P. Waterman, pers. comm.).

Alkaloids constitute the largest single class of secondary plant products in flowering plants (Levin and York, 1978). Because many alkaloids are potent poisons, they play a prominent role in plant chemical defense (Rhoades and Cates, 1976). The toxicity of alkaloids from tropical plants is greater than those from temperate plants (Levin and York, 1978). Phytochemical screening studies in Malaysia (Carrick et al., 1968; Chan and Teo, 1969, 1972; Chan et al., 1977) indicate that 11 to 22% of the forest plants contain alkaloids. Gartlan et al. (1980) found that 8% of the trees sampled at Douala-Edea contained alkaloids compared with 37% at Kibale.

Plants may use low nutrient quality (Moran and Hamilton, 1980) or poor digestibility (Van Soest, 1982) as a defense against herbivores. By providing a low supply of nutrients or making them difficult to extract, plants present a potential food source that yields a lower net benefit to an animal. Often plants may sustain growth on levels of mineral that will not support animal growth (Van Soest, 1982). Mature leaf foliage from a variety of Endau-Rompin plants contained consistantly low concentartions of mineral nutrients, indicating a forage of low nutritive quality. Phosphorus content was quite low ($\bar{x}$=0.066%, n=93), especially compared with calcium ($\bar{x}$=0.74%, n=93) (Ca:P ratio = 11:1). Crude protein content was also low ($\bar{x}$=10.2%, n=93) compared with other rain forest sites (P. Waterman, pers. comm.). In addition, protein availability was probably reduced by the high tannin content. High concentrations of structural carbohydrates and lignin, expressed as ADF, further reduced forage quality. Cellulose can be degraded only by microbes; lignin is undigestible (Van Soest, 1982). Endau-Rompin foliage averaged 49% ADF, indicating high fiber content and low digestibility (Waterman et al., 1980).

Stem material was consistantly poorer quality forage compared with mature leaves. Concentrations of crude protein, ash, and minerals were substantially higher in mature leaves. Percent composition of fiber in stems was 16% more than in mature leaves. The only indicator of poor quality forage higher in mature leaves than stems was the condensed tannin assay.

Forest gaps play a prominent role in the successional dynamics of tropical rain forests (Hartshorn, 1978; Whitmore, 1978). These gaps, created by the death and collapse of large forest trees, are filled by juvenile trees growing in the understory or by invading species. As the understory trees grow to maturity, the gap is closed and the rebuilding forest returns to the mature closed-canopy phase. Primary forest consists of a near random mosaic of gap, rebuilding, and mature successional stages. Gaps in the forest canopy provide a better growing environment for many plants. The quantity and quality of light reaching the understory are increased, and nutrients are released as dead plants decay. Also, a temporary decrease in root competition occurs. Gap size has an important influence on species composition and growth rates. In small gaps, existing shade-tolerant seedlings and saplings commence more rapid growth. Larger gaps encourage the establishment of more light-demanding species, plants more typical of secondary forests. Often, these pioneer species form small monotypic stands, especially in large openings (Whitmore, 1975).

Experimental research suggests pioneer plants are more palatable to generalist herbivores than late successional plants (Cates and Orians, 1975; Coley, 1980; Hartshorn, 1978), though exceptions exist (Otte, 1975; Majorana, 1977). Generally, late successional species are more apparent in the habitat (Feeny, 1976). Thus, they are expected to contain greater concentrations of defensive chemicals, particularly substances that reduce digestibility (Feeny, 1976). In contrast, rapidly growing pioneer plants should contain higher concentrations of soluble cell contents and less fiber. Because of the high metabolic cost of tannins, pioneers may depend on small quantities of plant toxins (i.e. alkaloids, saponins, etc.) for chemical defense (Rhoades and Cates, 1976).

About 15% of the Selai study site was in the gap successional stage. The remainder of the forest was in a closed-canopy phase, either rebuilding or mature. All gaps were small in area (<0.1 ha), created by a single or multiple tree falls, and widely scattered. Because of their small size, most gaps contained plants typical of the adjacent forest understory. Clumps of pioneers, especially *Macaranga* sp., were found only along river banks.

All animals must capture nutrients to live and leave offspring. Optimal foraging theory attempts to explain and predict many aspects of foraging behavior (see Pyke et al., 1977). Natural selection should favor animals that maximize their rate of net intake of positive nutrient, while avoiding toxic situations. As an animal forages, it chooses where to feed, what to eat, how long to stay in a habitat patch, and its path among habitat patches. Generally, a foraging animal should select habitats with the greatest abundance of preferred foods, choose foods that provide it with the greatest net benefit, feed in a habitat patch until its rate of food intake drops below some average, and move so that the maximum number of preferred foods are encountered (Pyke et al., 1977). Because of the complex chemical nature of vegetation, optimal foraging theory has been unable to adequately predict diets of large generalist herbivores (Westoby, 1974). Westoby (1974, 1977) suggests several factors that cause large generalist herbivores to select more diverse diets than optimal foraging theory would predict. Diverse diets in these animals, including rhinos, may result from them sampling plants for palatibility, balancing nutrition by mixing their diet, and selecting plants or plant parts based on changes in abundance or phenology.

Mammals possess morphological and physiological adaptations for a particular feeding habit, especially specializations of the dentition and digestive system. Ungulate evolution has resulted in 2 major groups, perissodactyls and artiodactyls, that arose from a common "proto-ungulate" ancestor (Janis, 1976). Although these 2 ungulate groups have different external morphological characteristics, the ecologically important difference is the anatomy of their digestive systems (Foose, 1982). In the artiodactyls, microbial fermentation of foods occurs in the rumen, a greatly enlarged and complicated forestomach. Consequently, ingested vegetation is subjected to microbial fermentation before reaching the normal sites of mammalian digestion and absorption in the stomach and intestines. The ruminent systems appears to maximize the extraction of energy and protein per unit of vegetation consumed, but the reticulo-omasal orifice retards the passage of fibrous particles through the gut (Van Soest, 1982). Also, gut microbes may be effective and versatile in detoxifying plant poisons (Freeland and Jansen, 1982). Because of the rumen´s forward position, plant toxins would be detoxified before they could be absorbed into the ungulate´s body.

In perissodactyls, fibrous materials are fermented by microbial activity in an enlarged colon and/or prominent cecum (Parra, 1978; Van Soest, 1982). The processes of fermentation are similiar in both groups, but in nonruminents the site is located after the normal sites of enzymatic digestion and absorption (Janis, 1976; Parra, 1978; Foose, 1982). Most soluble carbohydrates and proteins are digested prececally by enzymatic action (Parra, 1978). In general, nonruminants digest fiber to a lessor extent, but they can extract more nutrients per unit time by faster passage rates and greater intakes of forage (Parra, 1978; Foose, 1982). Also, nonruminents minimize nutrient requirements per unit weight by enlargement of their body sizes. Thus, the nonruminent system may be advantagous in highly fibrous vegetation (Foose, 1982), especially if foods are available in sufficient quantities. In regards to plant poisons, hindgut fermenters are at a disadvantage because ingested plant toxins can be absorbed into the animal´s body before encountering detoxifying microbes (Freeland and Janzen, 1974; Foose, 1982). Because the nonruminent system is less effective in detoxifying secondary plant compounds than the ruminent system, nonruminents would be expected to avoid or consume small amounts of potentially poisonous plants. On the other hand, their large body size may allow nonruminents to tolerate certain secondary plant compounds in the diet, especially the digestion-reducing compounds.

Sumatran rhinos, like all herbivores, are expected to select the least fibrous, most nutritious, least toxic plants available; but they are adapted to subsist on abundant, fibrous, low-quality forage.

Foose (1982) reports that browsing rhinos are adapted to eat highly lignified vegetation that contains abundant digestible cell solubles but little fermentable fiber. Because tropical rain forest understory foliage contains low concentrations of minerals and proteins and high amounts of fiber and secondary plant compounds, these rhinos would be expected to be selective in choosing foods, attempting to extract sufficient quantities of minerals and proteins while avoiding plant poisons.

The feeding behavior and diet of Sumatran rhinos in Endau-Rompin were similiar to those expected, given habitat conditions and feeding adaptations. Habitat and food selection were strongly influenced by their availability and quality. These rhinos were found to be animals of the hill forests, primarily occurring above 300 m. Within the Endau-Rompin region, rhino density was highest in hill forest habitats, although adjacent lowland habitats were also used (Flynn and Abdullah, 1983a). Elsewhere in Malaysia, Sumatran rhinos occurred mostly in hill forest habitats (Flynn and Abdullah, 1983b). In Sumatra, Borner (1978) found Sumatran rhinos using mostly hill and montane forest types, particularly in the mountainous Gunung Leuser Reserve. Historically, Sumatran rhinos were widely distributed, occurring in habitats ranging from coastal swamps to high mountains (Van Strien, 1974). Rhinos have been eliminated from most of their former range by hunting, leaving remnant populations. Human encroachment of lowland areas probably had a major impact on present rhino distribution. In Endau-Rompin, rhinos were gradually eliminated from most lowland areas with human encroachment, especially agricultural development and human settlement (Flynn and Abdullah, 1983a).

The selection of hill forest habitats may be influenced by behavioral factors. Hill forest sites are substantially cooler than adjacent lowland areas (Dale, 1963). The mean daily air temperature at the Selai base camp was 3 C cooler than at Segamat, a lowland site. Also, many suitable wallowing sites are available on the ridges and along the small streams of the study area. The lack of large predators, particularly tigers, in most hill forest sites may result in higher rhino survival there. Laurie (1978) reports that in Nepal and India tigers kill Indian rhino calves. Sumatran rhinos, being substantially smaller than Indian rhinos, would be susceptable to tiger predation until a greater age. Tigers were seldom observed in the hill forests of Endau-Rompin (Flynn, unpubl. data).

Within hill forest, rhinos selected habitats for feeding delineated by physiography and canopy cover. Stream bottom and lower slope physiographic types were selected for feeding; upper slopes were avoided. Stream bottoms contained a higher mean density of woody saplings and a greater amount of total leaf biomass, indicating a greater availability of food. Also, the density of certain principal food plants (i.e. *Prunus* sp. and *Eugenia* sp.) were higher in lower slope types. Although not specifically studied, foliage collected from stream bottom and lower slope types contained higher mean concentrations of minerals, suggesting a forage of higher nutritional quality. Alluvial soils in stream bottoms would be expected to contain more mineral nutrients than upland sites (Smallwood, 1966). Upper slopes were used mostly for travel; ridges were frequently used as travel corridors between drainages.

Talbot (1960) and Strickland (1967) stated that the Sumatran rhinoceros was an animal of secondary forest. Contrarily, I found them to select small forest gaps within primary forest for feeding sites. Selected forest gaps were always small (<0.1 ha), and plant composition within the gaps was not substantially different than the understory of the adjacent forest. Although gaps were selected for feeding, most of the feeding sites (59%) were in the closed-canopy forest, and most of the feeding cases (75%) were plants typical of closed-canopy forest. Gaps were widely scattered, almost randomly distributed in the forest, and occupied a small proportion (15%) of the available habitat. Thus feeding exclusively in gaps would require a significant amount of search time. Plants growing in gaps may be slightly more nutritious but probably not enough to warrant feeding exclusively in them. Many gap plants may use toxins as their chemical defense (Feeny, 1976; Hartshorn, 1978); thus, they may be avoided by rhinos. In large gaps or open areas (i.e. river banks) with small clumps of similiar species, multiple individuals of a species were seldom eaten at a feeding site. On several occassions, only 1 individual from a clump of Macaranga sp. was eaten. Only a few large openings occurred in the study area, and they were seldom used. In adjacent areas, feeding in large openings was sometimes encountered, but the areas were not far from primary forest. Feeding in large openings was probably done during the cooler portions of the day.

Sumatran rhinos were found to be generalist herbivores, feeding on a great variety of plant taxa in the forest understory. In 342 feeding cases, food plants were represented by 49 plant families, 102 genera, and from 156 to 181 species. An exhaustive list of plants eaten would probably contain nearly every species growing in the study area, but most would contribute little to diet proportions. Thus, simple plant lists provide little information on rhino feeding ecology. Although the diet contained a large number of plant taxa, 75% of the total bites were from 30 genera. These plant genera were considered the rhino´s principal food plants. Unfortunately, good information on the species composition of the understory was not available. The limited available information on understory composition indicated that some principal foods were relatively common in the understory, but most were relatively rare, comprising less than 1% of the stand.

Species diversity of rhino diets reflected diversity in the understory of tropical rain forests. The total number of plant species in the study area was unknown, but over 4100 species of woody plants have been collected in Peninsula Malaysia (Whitmore, 1972). Wyatt-Smith (1966) found over 210 species of trees (over 10 cm DBH)in a 1.6 ha plot of lowland forest. A nearby plot contained an almost completely different set of species. The large number of plant taxa in the diet indicated that many plants could be eaten by the rhinos, but the low use indices suggested that most plants were only sampled for palatability. Also, diet diversity suggested that the rhinos were attempting to mix their diet, probably to obtain a good balance of nutrients while avoiding toxic dosages of secondary plant compounds.

Woody plants, including shrubs, small trees, vines, and juveniles of overstory trees, were almost exclusively selected for forage. Although common in the understory, herbacious plants were only eaten once. Also, palms were seldom eaten. Generally, rhinos ate the food resource most available to a terrestrial herbivore. The mean density of woody saplings in the understory was 5370 stems/ha; the total leaf biomass was estimated at 390 kg/ha. Plants with woody stems greater than 3.5 cm were seldom selected for food. Apparently, larger stems were difficult to break or push to the ground.

By plant part, the rhino's diet consisted of mostly mature leaves; young leaves comprised a small proportion of the diet. Stem material was often eaten along with mature leaves. Rhinos seldom browsed stems larger than 5 mm in diameter, although size was quite variable. Generally, rhinos selected plant parts based on availability and nutritional quality. Young leaves were rare in the understory; stems were low in nutrients and high in fiber. Most arboreal folivores in rain forest habitats show a strong preference for young leaves, seeds, or fruits (Chivers, 1980; Oates et al., 1980; McKey et al., 1981). Fruits were also an important part of the rhinos diet, but amounts eaten were difficult to quantify. Most large fleshy fruits were eaten when available, especially mangos. Fruits and seeds are high in minerals and digestible energy (McKey, 1978), generally good food packets. Fruits may provide important accessory nutrients that subsidize digestion of the high-toxin low-nutrient leaf portion of the diet (McKey, 1978). Also, Foose (1982) states that the nonruminant digestive system is adapted to efficiently digest fruits. Apparently, Sumatran rhinos spend a considerable amount of time searching for fruiting trees. During a major fruiting period, rhino tracks frequently led to fruiting trees. On other occasions, rhino trails passed under trees that had been in fruit previously. Rhinos may be important seed dispersers for trees with large fleshy fruits.

Nutritional quality of the diet of Sumatran rhinos was generally low. Diet was characterized by low levels of minerals and crude protein, and high concentrations of fiber and phenolics. Phosphorus content was especially low (0.077%) and may have been a limiting factor. Although little information has been available on the nutritional requirements of rhinos, Robinson and Slade (1974) recommended that horses should have a diet containing about 0.45% phosphorus and calcium with a Ca:P ratio not exceeding 2:1. Low phosphorus levels in the diet have a substantial impact on recruitment in most mammals by reducing fertility in females and survival of young. Rhinos may have improved the mineral content of their diet by eating fruits. Crude protein content (11.3%) of the diet was relatively low, especially considering the high condensed tannin content (4.8%). By complexing with plant and animal proteins, tannins and phenolics probably reduced protein digestibility. Fiber, expressed as ADF, was high (45%) in the diet. Choo et al. (1981) found the ADF assay highly inversely correlated with dry matter digestibility. Because of digestive system adaptations, rhinos were able to exploit a high fiber diet. Apparently, rhinos were able to tolerate tannins and phenolic compounds in the diet, possibly by passing them quickly through the digestive system (Foose, 1982). Limited information from the literature suggested that the diet contained few plants with alkaloids or saponins.

Plant chemistry influenced food selction by Sumatran rhinos. Generally, rhinos ate available mature leaves that provided the best food packet. Mature leaves of certain food plants contained significantly higher mean concentrations of most minerals (ASH, P, Ca) and crude protein compared with plants collected randomly along transects. The mean content of ADF in food plants was substantially lower, indicating that fiber was a strong factor affecting food selection. Discriminant function analysis showed good separation between group centroids of principal food plants and non-food plants; plants contributing little to diet proportions were intermediate. Over 64% of the plant samples were classified accurately into their respective groups, based on plant chemistry, using DF analysis. In contrast to the other 2 groups, principal food plants lay in a chemical space that was high in minerals, N, and TP, but low in ADF and CT. Non-food plants were high in ADF and low in minerals and N. The DF analysis indicated that plants eaten in the greatest amounts contained more minerals and crude protein. Plants high in phenolic compounds were eaten, but plants high in condensed tannins were used less. Other phenolic compounds, expressed as TP, did not adversely affect food selection. Sometimes phenolic compounds complex with alkaloids to form insoluble tannins (Freeland and Janzen, 1974). Any detoxification of alkaloids may result in a plant being more palatable to a rhino, thus possibly acounting for the high phenolic content of the diet.

Although high in the diet, some plant taxa were below average in nutritional quality. Some plants, i.e. *Eugenia* sp. and *Prunus* sp., were relatively common in the understory. These plant taxa probably provided some net benefit to the animals without introducing plant toxins; their high availability made them suitable forage. Plants that were high in nutrient content but low in the diet probably contained plant toxins, or they were rare in the habitat.

In conclusion, Sumatran rhino feeding ecology was influenced by the availability and quality of foods. In general, mature leaves selected for food contained relatively high levels of most minerals and crude protein, but low amounts of fiber and condensed tannins. Leaves containing plant toxins were probably avoided. The high plant species diversity in the habitat resulted in the rhinos having a diverse diet. Also, diet diversity was probably influenced by the rhinos sampling plants for palatability, balancing the nutritional composition of their diet, and mixing their diet to avoid toxic dosages of secondary plant compounds.

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REFERENCES

Andau, P. and J. Payne. (1982). The plight of the Sumatran rhinoceros in Sabah. Sandakan, Malaysia, Sabah For. Dep. (Unpublished report).

Becker, P. (1981). Potential physical and chemical defences of Shorea seedling leaves against insects. Malay. For., 44, 346-356.

________. (1982). Protein-binding capacity in Shorea (Dipterocarpaceae) seedling leaves. J. Chem. Ecol., 8, 1353-1367.

Borner, M. (1978). A field study of the Sumatran rhinoceros. Ph.D. thesis. Univ. Basel, Switzerland.

Bryant, J. P. (1981). Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. Science, 213, 889-890.

Burkill, I. H. (1966). Dictionary of the economic products of the Malay Peninsula. Kuala Lumpur, Ministry of Agric. Reprinted.

Carrick, J., K. C. Chan, and H. T. Cheung. (1968). A new phytochemical screening of Malaya. I. Chemical screening. Chem. Pharm. Bull., 16, 113-118.

Cates, R. G. and G. H. Orians. (1975). Successional status and the palatability of plants to generalized herbivores. Ecology, 56, 410-418.

Chan, K. C. and L. E. Teo. (1969). A new phytochemical survey of Malaya. II. Chemical screening. Chem. Pharm. Bull., 17, 1284-1286.

________., and ________. (1972). A new phytochemical survey of Malaya. III. Chemical screening. Chem. Pharm. Bull., 20, 1582-1584.

________., Kok Fef Mak, and ________. (1977). A new pytochemical survey of Malaya. IV. Chemical screening. Chem. Pharm. Bull., 25, 1826-1829.

Chivers, D. (1980). Ed. Malayan forest primates. Ten years' study of tropical rain forest. New York, Pleum Press.

Choo, G. M., P. W. Waterman, D. B. McKey, and J. S. Gartlan. (1981). A simple enzyme assay for dry matter digestibility and its value in studying food selection by generalist herbivores. Oecologia (Berl.), 49, 170-178.

Coley, P. (1980). Effects of leaf age and life history patterns on herbivory. Nature, 284, 545-546.

Conry, P. (1981). Habitat selection and use by the Malayan gaur in central Pahang, Malaysia. M. S. thesis. Univ. Montana, Missoula.

Cooley, W. and P. Lohnes. (1971). Mulitivarite data analysis. New York, John Wiley and Sons.

Dale, W. (1959). The rainfall of Malaya. J. Trop. Geogr., 13, 23-37.

________. (1963). Surface temperatures in Malaya. J. Trop. Geogr., 17, 52-71.

Dixon, L. and J. Brown. (1979). BMDP biomedical programs: P series. Berkely, Univ. Calif.

Eisenberg, J. F. and R. W. Thorington. (1973). A preliminary analysis of a neotropical mammal fauna. Biotropica, 5, 150-162.

________., and G. M. McKay. (1974). Comparison of ungulate adaptions in the New World and Old World tropical forests with special reference to Ceylon and the rainforests of Central America. In The behavior of ungulates and its relation to management, ed. by V. Geist and F. Walter, 585-602. IUCN Publ. New Ser., 24. Morges, Switzerland.

________., and J. Seidensticker. (1976). Ungulates in southern Asia: a consideration of biomass estimates for selected habitats. Biol. Conserv., 10, 293-308.

Evans, G. H. (1905). Notes on rhinoceros in Burma. J. Bombay Nat. Hist. Soc., 16, 555-561.

Feeny, P. (1970). Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology, 51, 566-581.

________. (1976). Plant apparency and chemical defense. Recent Adv. Phytochem., 10, 1-40.

Flynn, R. (1978). The Sumatran rhinoceros in the Endau-Rompin National Park of Peninsular Malaysia. Malay. Nat., 4, 5-12.

________., and M. Tajuddin Abdullah. (1983a). Distribution and number of Sumatran rhinoceros in the Endau-Rompin region of Peninsular Malaysia. Malay. Nat. J., in press.

________., and _______. (1983b). The distribution and status of the Sumatran rhinoceros in Peninsular Malaysia. Biol. Conserv., in press.

Foose, T. (1982). Trophic strategies of ruminents and nonruminents. Ph.D. thesis. Univ. Chicago, Chicago, Illinois.

Forest Department. (1977). Forest resources of Peninsular Malaysia. Kuala Lumpur, Dep. For.

Freeland, W. and D. Janzen. (1974). Strategies in herbivory by mammals: the role of secondary plant compounds. Am. Nat., 108, 269-286.

Garten, C. T. (1978). Multivariate perspectives on the ecology of plant mineral element composition. Am. Nat., 112, 533-544.

Gartlan, J. S., P. G. Waterman, D. B. Mckey, C. N. Mbi, and T. T. Struhsaker. (1980). A comparative study of the phytochemistry of two African rainforets. Biochem. Systematics and Ecol., 8, 401-422.

Gobbett, J. and C. Hutchison. (1973). Eds. The geology of the Malay peninsula. New York, John Wiley and Sons.

Goddard, J. (1970). Food preferences of black rhinos in Tsavo National Park. East Afri. Wildl. J., 8, 145-161.

Groves, C. P. (1967). On the rhinoceros of Southeast Asia. Saugetierk. Mitt., 15, 221-237.

________., and F. Kurt. (1972). Di_cerorhinus sumatrensis_. Mammal. Species, 21. Am. Society Mammal.

Gyekis, K. (1966). Segamat District. Forest Reconnaissance Survey. For. Res. Inst. Rep. No. 7., Kepong, Malaysia.

Hartshorn, G. S. (1978). Tree falls and tropical forest dynamics. In Tropical trees as living systems, ed. by P. Tomlinson and M. Zimmermann, 617-638. New York, Cambridge Univ. Press.

Hobbs, N., D. Barker, J. Ellis, and D. Swift. (1981). Composition and quality of elk winter diets in Colorado. J. Wildl. Manage., 45, 156-171.

Hoogerwerf, A. (1970). Udjung Kulon. The land of the last Javan rhinoceros. Leiden, Brill.

Hubback, T. (1939). The Asiatic two-horned rhinoceros. J. Mammal., 20, 1-20.

James, F. C. and H. H. Shugart. (1970). A quantitative method of habitat description. Audubon Field Notes, 24, 727-736.

Janis, C. (1976). The evolutionary strategy of the equidae and the origions of rumen and cecal digestion. Evolution, 30, 757-774.

Janzen, D. (1977). Promising directions of study in tropical animal-plant interactions. Ann. Missouri Bot. Gard., 64, 706-736.

________. (1978). Complications in interpreting the chemical defense of trees against tropical arboreal plant-eating vertebrates. In The ecology of arboreal folivores, ed. by G. Montgomery, 78-84. Washington, Smithsonian Inst. Press.

________. (1981). Patterns of herbivory in a deciduous forest. Biotropica, 13, 271-282.

Jordon, C. F. and R. Herrera. (1981). Tropical rain forests: are nutrients really critical? Am. Nat., 117, 167-180.

Khan, Mohd. (1973). Studies of the seladang (Bos gaurus) in the state of Perak. Malay. Nat. J., 26, 163-169.

________. (1977). Utilization of plants and fruits by elephants. Malay. Nat. J., 30, 35-38.

Kochummen, K. M. and F. S. P. Ng. (1977). Natural plant succession after farming in Kepong. Malay. For., 40, 61-78.

Laurie, A. (1978). The ecology and behavior of the greater one-horned rhinoceros. Ph.D. thesis. Univ. Cambridge, UK.

________. (1982). Behavioral ecology of the greater one-horned rhinoceros. J. Zool., 196, 307-342.

Lee, D. (1980). The sinking ark. Kuala Lumpur, Heinemann Books.

Levin, D. A. (1971). Plant phenolics: an ecological perspective. Am. Nat., 105, 157-181.

________., and B. M. York. (1978). The toxicity of plant alkaloids: an ecological perspective. Biochem. Systematics and Ecol., 6, 61-76.

Maiorana, V. C. (1978). What kinds of plants do herbivores really prefer? Am. Nat., 112, 631-635.

Marcum, C. L. and D. O. Loftsgaarden. (1980). A nonmapping technique for studing habitat preferences. J. Wildl. Manage., 44, 963-968.

Martin, E. B. (1979). The international trade in rhinoceros products. Gland, Switzerland, WWF/IUCN.

McClure, H. (1966). Flowering, fruiting, and animals in the canopy of a tropical rain forest. Malay. For., 29, 182-203.

McKey, D. (1978). Soils, vegetation, and seed-eating by black colobus monkeys. In The ecology of arboreal folivores, ed. by G. Montgomery, 423-437. Washington, Smithsonian Inst. Press.

________., P. W. Waterman, C. N. Mbi, J. S. Gartlan, and T. S. Struhsaker. (1978). Phenolic content of vegetation in two African rain forests: ecological implications. Science, 202, 61-64.

________., J. S. Gartlan, P. W. Waterman, and G. M. Choo. (1981). Food selection by black colobus monkeys (Colobus satanas) in relation to plant chemistry. Biol. J. Linn. Soc., 16, 115-146.

McNeely, J. and A. Laurie. (1977). Rhinos in Thailand. Oryx, 13, 486-487.

Medway, L. (1969). The wild mammals of Malaya and Singapore. Kuala Lumpur, Oxford Press.

________. (1972). Phenology of a tropical rain forest in Malaya. Biol. J. Linn. Soc., 4, 117-146.

Moran, N. and W. Hamilton. (1980). Low nutritive quality as a defense against herbivores. J. Theor. Biol., 86, 247-254.

Morrison, D. (1967). Multivariate statistical methods. New York, McGraw-Hill.

Mueller-Dombois, D. and H. Ellenberg. (1974). Aims and methods of vegetation ecology. New York, John Wiley and Sons.

Nie, J., Hull, J. Jenkins, K. Steinbrenner, and D. Bent. (1975). Statistical package for the social sciences. Chicago, McGraw-Hill.

Oates, J. F., P. W. Waterman, and G. M. Choo. (1980). Food selection by the South Indian leaf-monkey, Presbytis johnii, in relation to leaf chemistry. Oecologia (Berl.), 45, 45-56.

Olivier, R. C. D. (1978). On the ecology of the Asian elephant Elephas maximus Linn. with particular reference to Malaya and Sri Lanka. Ph.D. thesis. Cambridge Univ., UK.

Otte, D. (1975). Plant preference and plant succession: a consideration of evolution of plant preference in Schistocerca. Oecologia (Berl.), 18, 129-144.

Owen-Smith, N. (1975). The social ethology of the white rhinoceros (Ceratotherium simum Burchell 1817). Z. Tierpsychol., 38, 337-384.

Parra, R. (1978). Comparision of foregut and hindgut fermentation in herbivores. In The ecology of arboreal folivores, ed. by G. Montgomery, 205-229. Washington, Smithsonian Inst. Press.

Peek, J. M., D. L. Urich, and R. Mackie. (1976). Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildl. Monogr., 65, 1-65.

Petrides, G. A. (1975). Principal foods versus preferred foods and their relations to stocking rate and range condition. Biol. Conserv., 7, 161-169.

Poore, M. (1963). Problems in the classification of tropical rain forest. J. Trop. Geogr., 17, 12-19.

________. (1968). Studies in Malaysian rain forest. I. The forest on the Triassic sediments in Jenka Forest Reserve. J. Ecol., 56, 143-196.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. (1977). Optimal foraging: A selective review of theory and tests. Q. Rev. Biol., 52, 137-154.

Raemaekers, J., F. P. Aldrich-Blake, and J. Payne. (1980). The forest. In Malayan forest primates. Ten years´ study in tropical rain forest, ed. by D. Chivers, 29-61. New York, Plenum Press.

Rhoades, D. and R. Cates. (1976). Toward a general theory of plant antiherbivore chemistry. Recent Adv. Phytochem., 10, 168-213.

Robinson, D. and L. Slade. (1974). The current status of knowledge on the nutrition of equines. J. Anim. Sci., 39, 1044-1066.

Rosenthal, G. and D. Janzen. (1979). Eds. Herbivores: Their interections with secondary plant metabolites. New York, Academic Press.

Richards, P. (1952). The tropical rain forest. Cambridge, Cambridge Univ. Press.

Schenkel, R. and L. Schenkel-Hulliger. (1969). The Javan rhinoceros in Udjung Kulon Nature Reserve. Its ecology and behavior. Acta Trop. (Basel) 26, 97-135.

Simon, N. Ed. (1969). Red data book, Mammalia. Gland, Switzerland, IUCN/WWF.

Smallwood, H. A. (1966). Schematic-reconnaissance soil survey of the Segamat-Gemas-Tangkak region of north Johor. Malay. Soil Surv. Rep. Kuala Lumpur, Malaysia, Dep. Agric.

Sokal, R. and F. J. Rohlf. (1969). Biometry. San Fransisco, W. H. Freeman and Co.

Stevens, W. E. (1968). The conservation of wildlife in West Malaysia. Kuala Lumpur, Malaysia, Dep. Wildl. and National Parks.

Strickland, D. (1967). Ecology of the rhinoceros in Malaya. Malay. Nat. J., 20, 1-17.

Symington, C. F. (1933). The study of secondary growth on rainforst sites in Malaya. Malay. For., 2, 107-117.

Talbot, L. (1960). A look at threatened species. Oryx, 5, 153-293.

Thom, W. (1935). Rhinoceros shooting in Burma. J. Bombay Nat. Hist. Soc., 38, 138-150.

Van Soest, P. J. (1982). Nutritional ecology of the ruminent. Corvallis, O and B Books.

Van Steenis, C. (1953). Flora Malesiana. Leiden, Noordhoff.

Van Strien, N. (1974). The Sumatran or two-horned Asiatic rhinoceros. A study of the literature. Meded. Landbouwhogeschool Wageningen, 14-16.

Waterman, P. W., C. N. Mbi, D. B. McKey, and J. S. Gartlan. (1980). African rainforest vegetation and rumen microbes: phenolic compounds and nutrients as correlates of digestibility. Oecologia (Berl.), 47, 22-33.

Weigum, L. (1972). The problems in the preservation of the seladang in the Malaysian national park. M. S. thesis. Mich. St. Univ., East Lansing.

Westoby, M. (1974). An analysis of diet selection by large generalist herbivores. Am. Nat., 108, 290-304.

________. (1978). What are the biological bases of varied diets? Am. Nat., 112, 627-631.

Whitmore, T. (1972). Tree flora of Malaya. Kuala Lumpur, Longman.

________. (1975). Tropical rain forests of the Far East. Oxford, Claredon Press.

_______. (1978). Gaps in the forest canopy. In Tropical trees as living systems, ed. by P. Tomlinson and M. Zimmermann, 639-655. New York, Cambridge Univ. Press.

Williams, K. and G. Petrides. (1980). Browse use, feeding behavior, and management of the Malayan tapir. J. Wildl. Manage., 44, 489-493.

Womersley, J. (1969). Plant collecting for anthropologist, geographers, and ecologists in New Guinea. Port Morsby, Papuau New Guinea, Dep. For.

Wyatt-Smith, J. (1964). A preliminary vegetation map of Malaya with descriptions of the vegetation types. J. Trop. Geogr., 18, 200-213.

________. (1966). Ecological studies on Malayan forests. Malay. For. Dep. Res. Rep. 52. Kuala Lumpur, Malaysia, Dep. For.

________., and K. Kochummen. (1979). Pocket check list of the timber trees. Malay. For. Rec. No. 17. Kuala Lumpur, Dep. For.

APPENDIX A

PLANT TAXA RECORDED AS EATEN BY SUMATRAN RHINOCEROS IN THE ENDAU-ROMPIN AREA, SOUTHERN PENINSULAR MALAYSIA.

Scientific name	Number of Feeding cases
Aceraceae	
Acer laurinum	2
Actinidiaceae	
Saurauia sp.	3
Alangiaceae	
Alangium ebenaceum	1
Annonaceae	
Goniothalamus sp.	1
Monocarpia marginalis	1
Polyalthia glauca	1
Apocynaceae	
Tabernaemontana sp.	1
Aquifoliaceae	
Ilex macrophylla	1
Araceae	
Homalomena rubra	1
Burseraceae	
Dacryodes laxa	1
D. rugosa	1
Celastraceae	
Ehesa paniculata	4
Glyptopetalum fruticosum	2
Lophopetalum floribundum	1
Convolvulaceae	
Erycibe sp.	1

Appendix A (Cont'd).

Scientific name	Number of feeding cases
Dichapetalaceae	
Dichapetalum sp.	1
Dipterocarpaceae	
Hopea nutans	1
Hopea sp.	1
Shorea leprosula	1
S. maxima	1
S. parvifolia	2
Ebenaceae	
Diospyros subrhomboidea	1
D. wallichii	1
Diospyros sp.	6
Elaeocarpaceae	
Elaeocarpus petiolatus	1
Elaeocarpus sp.	1
Euphorbiaceae	
Antidesma cuspidatum	1
A. velutinosum	1
Antidesma sp.	3
Aporusa sp.	7
Baccaurea lanceolata	1
Croton laevifolius	1
Elateriospermum tapos	1
Glochidion hypoleucum	2
Glochidan sp.	1
Macaranga hosei	1
M. laciniata	2
M. pruinosa	4
M. triloba	2
Pimelodendron griffithianum	1
Trigonopleura malayana	1
Fagaceae	
Lithocarpus sp.	1
Quercus oidocarpa	3
Flacourtiaceae	
Casearia lobbiana	1
Flacourtia sp.	2
Homalium sp.	1

Appendix A (Cont'd).

Scientific name	Number of feeding cases
Gnetaceae	
Gnetum sp.	1
Guttiferae	
Calophyllum sp.	1
Garcinia forbesii	1
G. griffithii	1
Garcinia sp.	2
Hyperiacaceae	
Cratoxylum formosum	1
Icacinaceae	
Gonocaryum gracile	1
Medusanthera gracilis	7
Medusanthera sp.	4
Stemonurus secundiflorus	1
Lauraceae	
Cinnamomum iners	1
Endiandra kingiana	1
Endiandra sp.	1
Litsea amara	1
L. nidularis	2
Litsea sp.	4
Nothophoebe sp.	1
Leeaceae	
Leea indica	1
Leguminosae	
Cynometra cauliflora	1
Pithecellobium clypearia	1
P. ellipticum	4
Loganiaceae	
Fagraea racemosa	2
Melastomataceae	
Melastoma malabathricum	1
Melastoma sp.	1
Phyllagathis rotundifolia	1
Meliaceae	
Aglaia griffithii	1
A. tenuicaulis	1
Aglaia sp.	7

Appendix A (Cont'd).

Scientific name	Number of feeding cases
Aphanamixis rohituka	1
Chisocheton sp.	1
Dysoxylum sp.	4
Menispermaceae	
Tinomiscium petiolare	2
Moraceae	
Artocarpus elasticus	1
A. nitidus	2
A. rigidus	1
Ficus chartacea	4
F. depressa	1
F. fistulosa	1
F. grossularioides	1
F. schwarzii	1
F. sinuata	1
F. uniglandulosa	1
F. vasculosa	1
F. vrieseana	2
Ficus sp.	6
Streblus elongatus	1
Myristicaceae	
Gymnacranthera forbesii	3
Knema curtisii	1
K. malayana	1
Myrsinaceae	
Ardisia colorata	3
A. oxyphylla	1
Ardisia sp.	3
Maesa ramentacea	5
Myrtaceae	
Eugenia anisosepala	1
E. cerasiformis	1
E. densiflora	1
E. syzygioides	2
Eugenia sp.	7
Oleaceae	
Chionanthus lamosa	1
C. oliganthus	2
C. ramiflorus	1
Chionanthus sp.	2

Appendix A (Cont'd).

Scientific names	Number of feeding cases
Palmae	
Calamus sp.	1
Korthalsia sp.	1
Polygalaceae	
Xanthophyllum sp.	1
Rhizophoraceae	
Anisophyllea grandis	1
Gynotroches axillaris	1
Pellacalyx saccardianus	2
Pellacalyx sp.	1
Rosaceae	
Prunus arborea	36
P. grisea	1
P. malayana	5
P. odorata	1
P. polystachya	2
Prunus sp.	1
Rubiaceae	
Amaracarpus caudatus	1
Amaracarpus sp.	1
Gardenia sp.	4
Lasianthus sp.	7
Mycetia sp.	1
Pavetta indica	15
Pavetta sp.	1
Randia scortechini	2
Randia sp.	2
Timonius sp.	1
Uncaria sp.	2
Urophyllum glabrum	2
Urophyllum sp.	7
Rutaceae	
Acronychia porteri	1
Atalantia roxburghiana	1
Luvunga scandens	1
Luvunga sp.	1
Tetractomia sp.	1
Sapindaceae	
Arytera sp.	1
Mischocarpus sp.	1

Appendix A (Cont'd).

Scientific names	Number of feeding cases
Pometia pinnata	1
Xerospermum wallichii	5
Sapotaceae	
Madhuca korthalsii	1
Palaquium hexandrum	2
P. rostratum	2
Palaquium sp.	2
Payena lucida	2
Simaroubaceae	
Quassia indica	1
Sterculiaceae	
Sterculia sp.	1
Styraceae	
Styrax benzoin	1
Symplocaceae	
Symplocos adenophylla	1
Theaceae	
Adinandra acuminata	2
Adinandra sp.	
Ternstroemia penangiana	1
Tiliaceae	
Grewia laurifolia	1
G. paniculata	1
Grewia sp.	2
Ulmaceae	
Gironniera nervosa	1
G. subaequalis	1
Verbenaceae	
Callicarpa sp.	2
Clerodendrum villosum	3
Clerodendrum sp.	2
Congea forbessii	1

APPENDIX B

CHEMICAL COMPOSITION OF CERTAIN SUMATRAN RHINO FOOD PLANTS. SAMPLES CONTAINED ONLY MATURE LEAF MATERIAL. VALUES EXPRESSED AS PERCENT DRY MATTER.

Plant taxa	ASH	N	P	Ca	K	Mg	TP	CT	ADF
Acer laurinum	5.55	1.45	0.084	0.59	0.96	0.24	15.59	1.71	39.54
A. laurinum	8.73	1.72	0.098	2.25	1.71	0.29	6.98	9.88	34.51
Aglaia griffithii	7.47	1.99	0.098	0.73	1.56	-	1.09	1.80	27.89
Aglaia sp.	2.92	1.65	0.054	0.25	0.99	0.22	-	-	-
Antidesma cuspidatum	6.09	1.54	0.058	2.25	0.77	-	8.98	5.33	49.96
A. velutinosum	9.70	1.67	0.075	0.77	1.24	-	9.17	2.89	36.50
Antidesma sp.	3.43	1.89	0.074	0.24	1.01	-	4.62	1.71	49.59
Aphanamixis rohituka	5.76	2.23	0.079	0.67	1.08	-	0.57	0.00	41.55
Ardisia colorata	7.89	1.70	0.061	0.89	1.58	-	9.07	7.28	67.64
A. colorata	5.79	1.95	0.065	0.60	1.36	-	9.07	7.28	42.58
A. oxyphylla	10.19	1.25	0.048	0.85	1.09	-	6.97	6.02	42.94
Ardisia sp.	2.94	2.47	0.038	0.35	0.91	0.31	-	-	-
Artocarpus rigidus	8.13	1.61	0.087	0.43	1.20	0.15	3.67	22.50	53.18
Arytera sp.	11.74	1.89	0.085	0.74	3.34	-	0.00	0.00	55.69
Baccaurea lanceolata	14.56	1.57	0.076	0.88	1.05	0.24	1.51	11.38	38.89
Bhesa paniculata	6.26	1.36	0.057	1.29	0.88	0.37	6.25	1.90	36.55
B. paniculata	6.59	1.44	0.072	1.96	0.64	-	6.82	8.96	27.19
B. paniculata	10.82	1.69	0.072	2.45	0.86	-	1.34	4.00	39.17
B. paniculata	7.47	1.77	0.059	1.24	0.81	-	3.48	4.16	38.14
Chionanthus oliganthus	8.33	1.41	0.076	0.45	0.92	-	1.90	2.31	38.32
Chisocheton sp.	6.62	1.61	0.088	1.28	0.68	-	5.96	4.65	50.08
Croton laevifolius	10.84	2.18	0.101	0.49	3.38	-	0.83	0.00	40.46
Cynometra cauliflora	9.93	1.91	0.069	0.70	1.02	-	-	-	-
Diospyros sp.	6.44	2.32	0.084	1.19	1.37	-	2.49	1.99	45.38
Diospyros sp.	4.96	1.98	0.068	0.53	1.15	-	1.91	1.27	58.18
Elaeocarpus petiolatus	4.27	2.03	0.041	1.00	0.54	0.24	-	-	-

Appendix B (Cont'd).

Plant taxa	ASH	N	P	Ca	K	Mg	TP	CT	ADF
Elaeocarpus sp.	4.50	1.62	0.048	1.14	0.38	0.28	-	-	-
Eugenia cerasiformis	5.44	1.19	0.059	0.72	0.96	-	5.74	3.47	42.21
Eugenia densiflora	6.26	1.10	0.041	0.74	0.65	0.26	12.14	0.71	29.72
Eugenia syzygiodes	4.95	1.31	0.056	0.61	0.57	-	-	-	-
Eugenia sp.	5.67	1.11	0.052	0.52	1.20	0.50	4.55	0.93	56.46
Eugenia sp.	2.48	1.38	0.070	0.46	0.46	-	4.54	1.78	57.32
Fagraea racemosa	8.91	3.20	0.110	2.30	1.60	-	1.81	0.00	34.41
F. racemosa	7.47	3.22	0.118	0.59	0.96	-	2.43	0.00	32.58
Ficus chartacea	12.05	1.79	0.082	1.45	1.80	0.76	-	-	-
F. chartacea	12.68	1.59	0.088	1.89	1.48	-	2.89	11.03	53.08
F. chartacea	12.74	1.96	0.094	2.15	1.70	-	1.39	0.99	43.53
F. chartacea	14.46	1.67	0.082	1.58	1.68	-	2.19	10.00	33.69
F. uniglandulosa	11.80	1.66	0.064	1.13	1.09	0.43	0.70	3.74	34.05
F. vasculosa	14.72	1.73	0.061	0.63	1.64	-	-	-	-
Ficus sp.	12.05	1.58	0.104	0.91	1.74	-	2.60	18.17	34.90
Ficus sp.	6.96	1.90	0.102	0.68	1.72	-	1.38	1.53	62.44
Flacourtia sp.	5.25	1.44	0.049	0.82	1.21	0.24	2.79	5.78	46.52
Garcinia forbesii	7.92	1.12	0.055	1.96	0.51	0.33	1.50	0.00	32.10
Gardenia sp.	6.43	1.77	0.061	1.15	1.62	0.25	-	-	-
Gioronniera nervosa	10.64	2.36	0.092	0.67	0.75	-	3.34	14.13	42.11
Glochidion sp.	3.85	2.33	0.071	0.45	0.80	-	6.20	7.79	62.59
Gonocaryum gracile	8.85	1.72	0.055	0.71	1.44	-	0.00	0.00	57.09
Gymnacranthera forbesii	5.26	1.28	0.067	0.77	1.13	6.37	3.47	9.21	49.89
G. forbesii	7.32	1.24	0.059	1.43	0.81	0.32	3.96	3.77	49.25
Gynotroches axillaris	10.16	1.69	0.057	0.68	0.89	0.23	2.36	12.50	49.64
Hopea nutans	3.84	1.49	0.060	0.81	0.83	-	1.61	2.28	50.73
Knema curtisii	6.64	1.84	0.074	0.63	1.36	-	0.28	1.24	47.60
K. malayana	2.77	1.68	0.039	0.26	0.78	0.25	2.95	15.79	64.77
Lasianthus sp.	11.57	1.73	0.053	0.40	0.84	0.53	-	-	-
Lasianthus sp.	3.66	1.68	0.043	0.74	0.37	0.35	1.38	3.35	30.84

Appendix B (Cont'd).

Plant taxa	ASH	N	P	Ca	K	Mg	TP	CT	ADF
Litsea amara	5.40	1.71	0.078	0.53	0.96	-	1.08	13.70	47.39
L. nidularis	5.88	1.49	0.058	0.54	1.33	-	1.55	2.90	68.19
Luvunga scandens	9.90	1.59	0.081	0.47	1.34	-	-	-	-
Macaranga pruinosa	5.58	1.64	0.095	0.80	0.72	-	10.67	2.83	43.69
M. triloba	5.29	1.51	0.078	0.80	0.74	-	14.69	2.57	35.27
Madhuca korthalsii	5.78	1.68	0.108	0.75	1.17	-	1.63	7.10	46.34
Maesa ramentacea	5.82	1.12	0.079	0.50	1.29	0.26	-	-	-
M. ramentacea	4.82	0.75	0.077	0.44	1.50	0.22	-	-	-
M. ramentacea	4.33	1.66	0.060	0.49	0.83	0.28	7.36	30.69	59.83
M. ramentacea	3.44	1.41	0.055	0.33	0.96	0.18	11.12	53.39	62.12
Medusanthera gracilis	8.14	2.28	0.067	0.93	1.36	0.52	-	-	-
M. gracilis	6.17	3.02	0.070	0.70	1.20	0.45	0.80	3.04	25.82
M. gracilis	9.56	2.89	0.094	1.20	1.48	0.37	1.44	3.57	35.17
M. gracilis	8.32	2.81	0.119	1.62	1.80	-	1.56	1.67	29.04
M. gracilis	9.61	3.44	0.084	0.76	1.63	-	0.27	0.00	34.43
M. gracilis	10.18	2.60	0.074	0.59	1.60	-	0.00	0.00	35.00
Mischocarpus sp.	10.76	1.82	0.075	0.63	3.21	-	0.00	0.00	56.09
Palaquium hexandrum	5.83	1.35	0.040	1.50	1.02	-	5.84	14.49	42.92
P. hexandrum	5.84	1.45	0.051	0.68	1.32	-	4.35	12.36	52.58
P. rostratum	4.89	1.35	0.033	0.84	0.83	0.38	-	-	-
Pavetta indica	6.93	2.38	0.088	1.16	1.16	0.39	1.80	0.00	31.96
P. indica	6.25	3.03	0.093	2.03	1.15	-	-	-	-
P. indica	8.30	3.03	0.136	1.02	1.44	-	2.08	0.67	32.51
Pimelodendron griffithianum	4.95	1.34	0.053	0.78	0.55	0.32	8.52	1.85	36.53
Pithecellobium ellipticum	3.49	2.55	0.071	0.51	0.89	0.28	-	-	-
Prunus arborea	3.69	2.51	0.034	0.60	0.57	0.29	-	-	-
P. arborea	3.76	1.26	0.045	0.44	0.96	0.34	3.97	11.15	51.68
P. arborea	5.35	1.30	0.041	0.36	0.69	0.25	6.70	14.82	66.70
P. arborea	6.34	1.23	0.038	0.54	0.77	0.34	7.31	16.48	32.57
P. arborea	4.75	1.29	0.043	0.68	0.86	0.39	4.88	9.72	40.32

Appendix B (Cont'd).

Plant taxa	ASH	N	P	Ca	K	Mg	TP	CT	ADF
Prunus arborea	5.38	1.36	0.051	0.75	0.93	0.29	-	-	-
P. arborea	4.06	1.27	0.041	0.74	0.85	0.36	-	-	-
P. arborea	4.47	1.25	0.044	0.62	0.97	0.29	-	-	-
P. arborea	3.82	1.31	0.048	0.32	1.03	0.32	-	-	-
P. arborea	3.66	1.37	0.043	0.53	0.80	0.31	4.12	8.60	54.27
P. arborea	3.80	1.12	0.036	0.51	0.89	0.40	-	-	-
P. arborea	3.46	1.21	0.038	0.48	0.89	0.30	-	-	-
P. arborea	5.24	1.39	0.051	0.46	1.35	-	2.29	7.35	51.56
P. arborea	4.76	1.27	0.043	0.66	1.06	-	-	-	-
P. arborea	5.06	1.43	0.050	0.47	1.05	-	1.10	2.20	52.17
P. arborea	10.40	1.21	0.039	0.58	0.68	-	6.32	13.94	45.45
P. arborea	5.59	1.28	0.040	0.63	0.82	-	2.83	5.87	56.91
P. arborea	15.04	1.16	0.037	0.55	0.54	-	-	-	-
P. arborea	5.16	1.35	0.050	0.40	0.90	-	1.65	1.52	68.11
P. arborea	4.31	1.39	0.057	0.71	0.89	-	4.29	8.93	48.19
P. arborea	5.23	1.31	0.050	0.37	1.09	-	2.82	4.46	61.87
P. malayana	2.79	1.51	0.046	0.28	0.72	0.28	-	-	-
P. malayana	3.69	1.72	0.047	0.52	0.86	0.28	-	-	-
Quercus oidocarpa	6.24	1.73	0.075	0.63	1.10	-	2.96	4.46	51.11
Randia scortechinii	7.22	1.54	0.073	0.79	1.48	-	4.58	24.53	37.98
Shorea leprosula	3.61	1.85	0.076	0.68	0.73	0.19	4.62	2.76	49.60
S. parvifolia	3.49	1.64	0.061	0.58	0.70	0.30	5.38	7.51	50.42
S. parvifolia	3.82	1.56	0.069	0.51	0.80	-	3.86	3.36	51.73
Streblus elongatus	10.79	1.46	0.070	0.83	1.33	-	2.34	1.35	41.81
Styrax benzoin	4.00	1.31	0.045	0.66	0.67	0.33	-	-	-
Ternstroemia penangiana	5.32	1.06	0.037	0.61	0.79	0.24	5.39	1.42	38.52
Timonius sp.	5.45	2.38	0.108	0.71	1.16	-	3.73	14.89	57.98
Trigonopleura malayana	5.40	1.40	0.072	0.58	1.01	-	5.49	3.40	63.32
Xerospermum wallichii	4.08	1.29	0.058	0.99	0.36	-	6.87	26.38	47.89
X. wallichii	4.16	1.28	0.059	0.52	0.55	-	3.90	14.92	39.09

APPENDIX C

CHEMICAL COMPOSITION OF MATURE LEAF MATERIAL COLLECTED FROM CERTAIN UNDERSTORY PLANTS SELECTED RANDOMLY ALONG TRANSECTS. VALUES EXPRESSED AS PERCENT DRY MATTER.

Plant taxa	ASH	N	P	Ca	K	TP	CT	ADF
Alangium ebenaceum	6.56	1.50	0.096	1.14	1.23	6.66	0.64	47.18
Casearia sp.	8.68	1.45	0.041	1.34	1.71	0.98	1.71	65.59
Chisocheton sp.	6.73	1.27	0.073	0.57	1.50	0.56	1.29	58.58
Cinnamomum iners	4.17	1.90	0.062	0.42	1.27	0.55	0.00	58.08
Cryptocarya rugulosa	4.68	1.38	0.049	0.42	0.90	3.41	7.72	70.46
Durio malaccensis	10.26	1.24	0.055	0.70	1.11	2.52	9.39	59.25
Erycibe sp.	10.65	1.23	0.047	1.23	1.62	2.94	0.60	51.31
Erycibe sp.	3.56	1.27	0.047	0.63	0.88	10.39	9.97	43.51
Gonystylus confusus	4.66	1.82	0.084	0.49	1.24	1.22	0.60	61.41
Gordonia sp.	3.76	1.22	0.039	0.37	0.64	5.28	1.53	30.90
Homalium sp.	6.40	1.38	0.059	0.66	1.37	4.94	2.31	39.50
Hullettia dumosa	6.07	1.52	0.052	0.41	0.72	0.55	0.60	57.49
Lithocarpus sp.	4.45	1.29	0.047	0.31	0.61	4.96	1.00	55.24
Memecylon sp.	5.94	1.20	0.049	0.67	0.41	3.88	2.00	46.10
Neoscortechina paniculata	5.34	1.25	0.052	0.53	0.97	2.54	12.85	59.59
Polyalthia sp.	8.50	1.71	0.057	0.39	1.17	2.57	2.79	64.30
Pterospermum javanicum	3.39	1.39	0.073	0.23	1.10	0.99	0.99	60.86
Rhodamnia cinerea	2.20	1.23	0.034	0.24	0.81	9.17	10.57	64.29
Shorea acuminata	3.48	1.66	0.078	0.61	0.47	5.52	2.49	53.73
S. ovalis	2.71	1.59	0.072	0.44	0.70	4.83	1.73	65.93
S. singkawang	1.77	1.37	0.057	0.32	0.56	7.02	8.00	65.65
Shorea sp.	8.72	1.58	0.048	0.38	0.51	5.03	3.28	46.76
Stemonurus sp.	8.52	1.26	0.062	1.45	1.92	1.41	0.00	47.70
Trigonostemon sp.	7.80	1.21	0.045	0.47	1.25	2.19	2.59	68.46
Xanthophyllum sp.	5.32	2.19	0.048	0.33	0.75	1.38	0.00	50.91
Xanthophyllum sp.	3.40	1.53	0.060	0.32	0.86	5.63	1.55	54.32
Xylopia magna	5.38	1.60	0.049	0.40	1.18	2.82	6.11	63.01